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ANALYSES MULTIDIMENSIONNELLES DES EFFETS DE LA ROTATION ET D'UN COMPOST URBAIN SUR LA SCLÉROTINIOSE DU SOJA ET LA SANTÉ DU SOL

Thèse présentée
à la Faculté des études supérieures de l'Université Laval
dans le cadre du programme de doctorat en biologie végétale
pour l'obtention du grade de Philosophiae Doctor (Ph. D.)

FACULTÉ DES SCIENCES DE L'AGRICULTURE ET DE L'ALIMENTATION
UNIVERSITÉ LAVAL
QUÉBEC

JANVIER 2005

À Danielle et à la vie, d'où qu'elle vienne...

Résumé court

Chez deux sols (loam argileux ou sableux), on a comparé l'effet de la monoculture de soja et de la rotation soja-maïs (2-3 ans de maïs puis 1-2 ans de soja), ainsi que l'effet d'un compost urbain et de la fertilisation minérale, sur la survie et la germination carpogénique des sclérotes du *Sclerotinia sclerotiorum* et sur la sclérotiniose du soja. Au site argileux, la rotation de 3-ans-de-maïs a réduit (effet suppressif) la gravité de la maladie par un rendement accru du soja et par la diminution du couvert de dicotylédones, alors que le compost a augmenté la maladie. L'azote était négativement corrélé à la survie des sclérotes sous fertilisation minérale. Au site sableux, l'interaction 3-ans-de-maïs x compost a réduit la maladie. La teneur en argile a favorisé la germination carpogénique et la gravité de sclérotiniose, alors qu'une stabilité structurale accrue et l'activité microbiologique étaient négativement corrélées à la germination. Cette étude approfondit les interactions entre pratiques culturales, santé du sol et couvert végétal, et contribue à mieux expliquer leurs effets propres et communs sur la sclérotiniose.

Résumé long

On a examiné l'effet de l'amendement de deux sols (loam argileux ou sableux) en compost urbain sur la survie et la germination carpogénique de sclérotes du *Sclerotinia sclerotiorum*. Chez ces deux sols, on a comparé l'effet de la monoculture du soja et de la rotation soja-maïs (2-3 ans de maïs puis 1-2 ans de soja), et l'effet du compost et de la fertilisation minérale, sur la survie et la germination des sclérotes et sur la gravité de la sclérotiniose du soja. L'effet des pratiques culturales sur les variables de sclérotiniose a été testé par permutations grâce au codage du plan d'ANOVA (MANOVA) par des variables muettes introduites en régressions multiples ou en analyses canoniques des redondances (ACR). On a construit des modèles minimaux de régression/ACR regroupant une sélection de variables (couvert végétal, physico-chimie, microbiologie du sol) qui expliquaient le mieux les variables de sclérotiniose. Par la forme partielle de la régression/ACR, on a divisé la variance des variables de sclérotiniose entre les matrices couvert végétal, physico-chimie et microbiologie du sol, coordonnées spatiales et pratiques culturales.

Au site argileux, la rotation 3-ans-de-maïs a réduit la gravité de maladie, alors que le compost l'augmentait. Au site sableux, l'interaction 3-ans-de-maïs x compost a réduit la gravité de maladie. Selon les modèles minimaux, la rotation a réduit la gravité au site argileux par un rendement accru du soja et par la diminution du couvert végétal de dicotylédones, couvert qui favorise la germination carpogénique du *Sclerotinia*. L'azote était négativement corrélé à la survie des sclérotes sous fertilisation minérale. Au site sableux, l'argile a favorisé la germination du *Sclerotinia* et la sclérotiniose, alors qu'une stabilité structurale accrue et l'activité microbiologique liées à la matière organique étaient négativement corrélées à la germination carpogénique. Au site argileux, selon la partition de variance, la structure spatiale des caractéristiques physico-chimiques du sol expliquait la survie et la germination carpogénique. Au site sableux, l'activité microbienne (abondance bactérienne, quotient de minéralisation du carbone) était négativement corrélée à la germination mais positivement corrélée à la survie des sclérotes. Cette étude approfondit les connaissances des interactions entre pratiques culturales, santé du sol et couvert végétal, et contribue à mieux expliquer leurs effets propres et communs sur la sclérotiniose.

Avant-propos

Cette thèse de doctorat a été réalisée dans le cadre du projet CORPAQ (Conseil des recherches en pêche et en agroalimentaire du Québec) intitulé "Étude épidémiologique et intégration de pratiques culturales dans la lutte à la sclérotiniose du soja", dont elle constitue l'essentiel des résultats. Ce projet était dirigé par M. Daniel Dostaler (Université Laval), également directeur de la thèse, avec la collaboration de madame Sylvie Rioux (CÉROM), codirectrice, M. Marc Laverdière (Université Laval), conseiller en physique du sol, et M. Adrien N'Dayegamiye (IRDA), conseiller en microbiologie du sol.

Les résultats présentés dans l'annexe C ont donné lieu à deux communications scientifiques réalisées par l'étudiant et présentées au congrès annuel de la Société canadienne de phytopathologie, qui se déroulait à Montréal du 22 au 25 juin 2003 et dont les résumés sont présentés à l'annexe A. L'expérience au laboratoire était présentée sous forme d'affiche (Rousseau et Schaefer, 2003) et l'expérience en cabinet de croissance sous forme de présentation orale (Rousseau et *al*., 2003). Les manuscrits d'articles qui constituent les trois chapitres de cette thèse ont été écrits par l'étudiant, sous la supervision de D. Dostaler et S. Rioux, co-auteurs. Les expériences qui ont donné lieu à ces articles ont été réalisées par l'étudiant. Le chapitre 1 sera soumis à la revue canadienne de phytopathologie, et les chapitres 2 et 3 à la revue Soil Biology and Biochemistry.

Je tiens à remercier particulièrement M. Daniel Borcard et M. Pierre Legendre (Université de Montréal) pour leur précieuse collaboration à la résolution des problèmes de statistiques.

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INTRODUCTION

Le *Sclerotinia sclerotiorum* (Lib.) de Bary est l'agent de la sclérotiniose du soja [*Glycine max* (L.) Merr.]. Au Québec, la sclérotiniose entraîne fréquemment des pertes de rendement de 20 % qui peuvent atteindre 100 % les années particulièrement favorables à la maladie (Hartman et *al.*, 1998; Purdy, 1979). La production de sclérotes, forme de conservation du *S. sclerotiorum* dans le sol, occasionne des infestations récurrentes au champ et réduit la qualité des semences. Hormis la résistance génétique (Cober et *al.*, 2003 ; Rousseau et *al*., 2004), la rotation culturale (Kurle et *al*., 2001) et le travail du sol (Garcia-Garza et *al*., 2002) sont les moyens de lutte les plus efficaces contre la sclérotiniose du soja.

La lutte culturale influence les conditions de survie et de germination carpogénique des sclérotes du *S. sclerotiorum* dans le sol et donc l'infection des plantes. Or, l'absence de données propres à la culture du soja au Québec ne permet ni d'apprécier les variables qui influencent le développement des épidémies, ni d'en prévoir les pertes. Cette étude vise l'acquisition de connaissances nouvelles pour mieux comprendre le développement du *S. sclerotiorum* chez le soja et vise la promotion de moyens de lutte culturaux à la sclérotiniose.

D'une part, il n'y a pas d'étude réalisée au Canada sur la fertilisation organique avec du compost et son interaction avec la rotation culturale dans la lutte à la sclérotiniose du soja. D'autre part, la recherche qui allie phytopathologie et « santé du sol », concept qui repose sur des caractères ou des indicateurs physico-chimiques, biochimiques ou encore microbiologiques, est une préoccupation relativement nouvelle de la communauté scientifique. Aussi, cette recherche doctorale repose-t-elle sur l'hypothèse que: l'amendement en compost urbain et la rotation culturale maïs-soja agissent sur le développement du *S. sclerotiorum* et de la sclérotiniose du soja et modifient les propriétés du sol. Cette hypothèse est associée aux objectifs suivants:

1. comparer chez deux sols au champ, les effets d'une part, de la monoculture du soja et de la rotation avec le maïs et d'autre part, du compost urbain et de la fertilisation minérale sur la survie et la germination carpogénique des sclérotes du *S. sclerotiorum* et sur le développement de la sclérotiniose du soja

2. identifier des facteurs de risque associés à la sclérotiniose par le suivi de variables diversifiées de l'agroécosystème (variables de phénologie du soja, biomasse des adventices, activité de la microflore tellurique et caractéristiques physico-chimiques des sols) et étudier leur potentiel comme indicateurs de la santé du sol

3. examiner le potentiel de l'analyse canonique des redondances (Legendre et Legendre, 1998) pour étudier l'effet de la structure spatiale des données et répondre aux objectifs 1 et 2: i) tester par permutations les effets de la rotation et de la fertilisation selon un plan d'ANOVA (MANOVA) et calculer leurs contributions respectives à la variance de la survie, de la germination carpogénique des sclérotes et de la sclérotiniose; ii) proposer des modèles minimaux qui regroupent les variables de l'agroécosystème qui expliquent le mieux les variables de la sclérotiniose; iii) préciser les interactions entre d'une part, les indicateurs potentiels de la santé du sol et d'autre part, la lutte culturale et le développement de la sclérotiniose.

Cette thèse comprend une revue bibliographique, trois chapitres de recherche ainsi qu'une discussion générale et des conclusions. Les chapitres de recherche (1 à 3) abordent des aspects complémentaires de l'impact de la fertilisation organique avec un compost urbain et de la rotation culturale sur le *S. sclerotiorum* et le développement de la sclérotiniose du soja. Le chapitre 1 présente l'expérience principale intitulée : *Effet de la rotation et de l'amendement en compost urbain sur la sclérotiniose du soja dans deux sols*. Au chapitre 2, par une approche additive de l'analyse canonique des redondances (ACR) et de sa forme partielle, on construit des modèles multivariables minimaux qui expliquent les variables de sclérotiniose par les variables de l'agroécosystème en maintenant constant l'effet de la rotation et du compost urbain ou de la structure spatiale. Enfin, par une approche de partition de la variance à l'aide de l'ACR et de sa forme partielle, le chapitre 3 présente une décomposition de la variance des variables de sclérotiniose entre les groupes de variables qui caractérisent l'agroécosystème, la rotation ou l'amendement en compost urbain et les variables de la structure spatiale. La thèse se termine par une discussion générale, des conclusions et des perspectives.

En somme, cette étude vise à mieux comprendre les relations entre la lutte culturale à la sclérotiniose du soja et la santé du sol. Des indicateurs de la santé des sols sont utilisés pour identifier et quantifier les changements des caractéristiques des sols entraînés par la rotation et

l'amendement en compost urbain. L'approche multivariable, par des méthodes telles la régression multiple et l'analyse canonique des redondances (ACR), est utilisée pour préciser la nature des liens entre la santé du sol et la santé de la plante, liens qui font partie intégrante de la définition de la santé des sols (Doran et Zeiss, 2000).

REVUE BIBLIOGRAPHIQUE

1. La sclérotiniose du soja

La culture du soja s'est développée au Québec au cours de la dernière décennie. Cette plante de la famille des légumineuses, caractérisée par la fixation symbiotique de l'azote (N), laisse dans le sol près de 20 kg d'N organique par ha (Paré et *al.*, 1993). Pour cette raison, et parce que cette culture offre une couverture complète du sol, le soja s'insère très bien dans les rotations avec le maïs et les céréales. Or, l'intensification de la culture du soja a conduit au développement de la sclérotiniose, une maladie aussi appelée pourriture à sclérotes ou moisissure blanche. Les sclérotes du *S. sclerotiorum* peuvent survivre au-delà de 5 ans dans le sol (Boland et Hall, 1988a; Huang et *al.*, 1998) et infecter les cultures sensibles subséquentes. Cette persistance du *S. sclerotiorum* dans le sol en font le premier problème phytosanitaire dans la culture du soja au Québec.

On attribue habituellement le développement de la sclérotiniose chez le soja à des rotations inappropriées (Anderson, 1996) et plus généralement à l'abandon de la fertilisation organique (Asirifi et *al.*, 1994). Malgré l'efficacité de certains fongicides (Merriman et *al.*, 1979) contre le *S. sclerotiorum*, leur utilisation n'est pas économiquement envisageable en grandes cultures. Les données disponibles sur la survie des sclérotes à la surface du sol (Mitchell et Wheeler, 1990), les effets des pratiques culturales (Williams et Stelfox, 1980) ainsi que les résultats d'un projet antérieur (CORPAQ # 4575), sous la direction de S. Rioux (Rioux, 1998) montrent que, hormis la résistance génétique, le travail réduit associé aux rotations constitue l'essentiel de la lutte aux infestations de sclérotiniose chez le soja (Maheu, 1999; Rioux, 1997). Aux États-Unis, la résistance génétique demeure le moyen de lutte le plus efficace contre la sclérotiniose du soja avant même la rotation avec une espèce non-hôte (Kurle et *al*., 2001). Selon Wegulo et *al.* (1998) d'une part, aucune lignée de soja n'a montré de résistance complète au *S. sclerotiorum*; d'autre part, Rioux (1998) et Rousseau et *al*. (2004) montrent aussi que quelques lignées et cultivars de soja disponibles au Québec s'avèrent plus résistants que d'autres au *S. sclerotiorum*.

1.1 Le genre *Sclerotinia*

Le *Sclerotinia sclerotiorum*, discomycète tellurique, fait partie de la famille des Sclérotiniacées (Achbani et *al.*, 1995) à laquelle appartiennent aussi les genres *Botryosphaera* et *Monilinia*. Les *Sclerotinia* spp. forment des sclérotes de couleur blanc crème à noir dont la taille et la forme sont très variables. Chez le *S. sclerotiorum*, les sclérotes sont noirs, durs, plus ou moins ronds ou allongés et mesurent de 2 à 20 mm. Plus de 250 espèces de *Sclerotinia* ont été décrites. Depuis quelques années, la nomenclature de Kohn (1979) fait généralement consensus. Le genre comporte trois espèces pathogènes des grandes cultures: les *S. sclerotiorum*, *S. minor* Jagger, et *S. trifoliorum* Erikss.

1.2 Cycle évolutif et symptomatologie

Les sclérotes sont des structures de conservation qui persistent dans le sol au moins 5 ans chez le *S. sclerotiorum* (Boland et Hall, 1988a; Huang et *al.*, 1998). Le genre *Sclerotinia* a deux formes évolutives (Briard et *al.*, 1997). L'une est végétative: les sclérotes germent directement sous forme d'hyphes mycéliens. L'autre est méïosporée: les sclérotes forment des apothécies (de 5 à 15 mm de diamètre chez le *S. sclerotiorum*) qui, à maturité, libèrent des ascospores (méïospores endogènes). Les ascospores anémophiles se déposent sur la plante. Chez le soja, le *S. sclerotiorum* pénètre surtout par les pétales, envahit rapidement la fleur puis le pédoncule floral. Lorsque la lésion et le mycélium atteignent la tige, le transport de l'eau et des nutriments par les tissus vasculaires est affecté (Sinclair et Backman, 1989), voire interrompu. Les lésions brun clair à la surface des tiges se couvrent rapidement de mycélium blanc (Boland et Hall, 1988a). Leur marge peut être teintée de rouge ou de brun rougeâtre associés à une accumulation de pigments par la plante (Cline et Jacobsen, 1983; Grau et Bissonnette, 1974). Ces lésions apparaissent généralement à l'aisselle des premières grappes de fleurs. Le mycélium peut envahir la totalité de la tige et des rameaux latéraux (Boland et Hall, 1988a), la colonisation de la tige se faisant vers le haut (acropète) et vers le bas (basipète) (Grau et *al.*, 1982; Lumsden, 1979). La plante flétrit quelques semaines après l'infection initiale, au stade de pleine floraison ou d'apparition des premières gousses (R2 ou R3, selon l'échelle de Fehr et *al.*, 1971) (Boland et Hall, 1988b; Sinclair et Backman, 1989). Le développement des gousses situées au-dessus du ou des noeuds infectés et le remplissage des graines peuvent être fortement affectés (Grau et *al.*, 1982): les gousses sont réduites voire absentes, les graines sont blanchies, atrophiées et peuvent être remplacées par des sclérotes.

1.3 Épidémiologie: survie et germination des sclérotes du *Sclerotinia sclerotiorum*

La durée de la survie des sclérotes dans le sol varie en fonction de la profondeur d'enfouissement et des conditions d'humidité et de température (Adams, 1975; Cook et *al*., 1975) et peut excéder 5 ans (Hall, 1994). La conservation des sclérotes est optimale au-dessous de 0°C et leur dégradation augmente rapidement lorsque la température s'élève au-dessus de 0°C (Huang et Kozub, 1994). Smith (1972) rapporte que les sclérotes séchés se dégradent rapidement après réhydratation contrairement aux sclérotes restés humides, ce qui expliquerait leur meilleure survie en profondeur. En effet, laissés à la surface du sol, les sclérotes sont détruits après 18 mois, tandis que lorsqu'enfouis de 5 à 50 cm dans le sol, ils peuvent se conserver plus de 2 ans (Butzen, 1997; Yorinori et Homechin, 1984). Les cycles humidification-dessiccation, plus marqués à la surface du sol, seraient le principal facteur de destruction des sclérotes restés en surface. En effet, les travaux de Smith (1972) indiquent que des sclérotes non séchés se conservent mieux (0-6 % de dégradation) que ceux qui ont été séchés puis réhydratés (détruits à 78-100 %). Smith (1972) suggère que la perte de nutriments lors de la réhydratation stimulerait les micro-organismes hyperparasites en présence.

Les sclérotes ont besoin d'un conditionnement particulier pour lever leur dormance: un sol très humide (-25 kPa ou à saturation), des températures relativement basses (4-16°C) pendant 10 à 14 jours sont les conditions idéales (Grau, 1989). In vitro, les sclérotes exposés 8 semaines à de telles conditions fructifient mieux qu'après une exposition de 1 à 4 semaines (Dillard et *al*., 1995). Dillard et *al*. (1995) suggèrent que c'est le lessivage de probables molécules inhibitrices de la germination situées en surface ou à l'intérieur des sclérotes qui permettrait de lever la dormance. Cette hypothèse s'appuie sur l'absence de germination carpogénique chez les sclérotes conditionnés en environnement sec (Dillard et *al.*, 1995). Or, les conditions de fructification s'avèrent très variables selon les méthodes d'étude utilisées et la texture du sol (Teo et Morrall, 1985a). De même, les conditions de survie sont très variables et les résultats ne peuvent être extrapolés d'un sol à l'autre (Mitchell et Wheeler, 1990). Une seule étude montre que la survie à long terme (8 ans) des sclérotes du *S. sclerotiorum* dans deux types de sol (loam argileux et loess) en culture de laitue suit une distribution connue dite de Weibull (Ben Yephet et *al.*, 1993).

Pour produire des apothécies, les sclérotes ont besoin de lumière (12 h de photopériode au laboratoire), d'un potentiel hydrique supérieur à -500 kPa (ou la capacité au champ) pendant 16 jours et de températures entre 11 et 20°C (Hall, 1994). Selon Sun et Yang (2000), l'intensité lumineuse et l'humidité du sol interagissent avec la température optimale de fructification carpogénique et la rapidité de celle-ci. Le nombre de degrés-jours est positivement corrélé au nombre d'apothécies formées.

Au champ, les apothécies sont produites par les sclérotes situés dans les 5 premiers cm du sol et ne se développent généralement pas avant la fermeture du couvert végétal qui leur procure un microclimat frais et humide (Schwartz et Steadman, 1978). Les apothécies formées libèrent les ascospores généralement par bouffées suite à des perturbations physiques ou des variations de l'humidité relative (Schwartz et Steadman, 1978). Workneh et Yang (2000) ont vérifié dans le centre nord des États-Unis (Illinois, Iowa, Minnesota, Missouri et Ohio) que l'intensité de la sclérotiniose était plus forte lorsque les températures moyennes de début de saison (début juillet) étaient en-dessous des normales saisonnières. Au champ, les apothécies peuvent libérer continuellement des ascospores pendant plus de 10 jours (Henderson, 1962) à raison de $2{,}3 \times 10^6$ ascospores par apothécie (Schwartz et Steadman, 1978).

2. La qualité ou la santé du sol

Les concepts et les indicateurs de la santé des sols ou de qualité des sols ont été l'objet de recherches expérimentales et d'articles de synthèse tant ailleurs dans le monde (Anderson, 2003; Büchs, 2003; Karlen et *al*., 2003; Ruf et *al*., 2003; Schloter et *al*., 2003; Sherwood et Uphoff, 2000) qu'au Canada (Carter et *al*., 2002). Or, définir et estimer la santé du sol ("Soil health", Doran et Safley, 1997; Nielsen et Winding, 2002) est une préoccupation relativement nouvelle de la communauté scientifique. Si la santé du sol apparaît aujourd'hui tellement incontournable, c'est probablement dû à la négligence des intervenants, négligence qui a mis en péril les équilibres naturels de la biosphère (Doran et Zeiss, 2000), voire "la survie de l'espèce humaine" (Reeves, 2003).

Feller et *al*. (2003) rapportent que Albrecht Thaër (1752-1828), le fondateur de la "Théorie de l'humus", a élaboré une échelle de fertilité quantifiée des sols. Cette échelle comprend plusieurs "degrés de fécondité du sol" et est basée sur les propriétés du sol, les besoins de la plante, les

pratiques culturales, et la succession des cultures. Ces degrés réfèrent à la productivité pour une céréale standard ou de référence, le seigle. D'après Feller et *al*. (2003), cette échelle a été utilisée pendant une cinquantaine d'années pour évaluer les systèmes agricoles en Allemagne, puis est tombée dans l'oubli en raison du discrédit qui a frappé Thaër suite à la publication par Justus Von Liebig en 1855 de la théorie de la nutrition minérale qui semblait invalider totalement la théorie de l'humus. Les définitions les plus récentes de la qualité ou de la santé des sols reprennent cette approche globale de Thaër dans laquelle à la fois la productivité agricole et l'environnement sont pris en compte. Doran et Safley (1997) et Doran et Zeiss (2000) définissent la santé du sol comme "la capacité soutenue du sol à fonctionner comme un système vivant à l'intérieur des limites de l'écosystème et de l'utilisation du territoire, à soutenir la productivité biologique, à promouvoir la qualité de l'air et de l'eau, et à maintenir la santé des plantes, des animaux et des humains". Cette définition établit une différence entre la santé du sol et la qualité du sol généralement employées comme synonymes (USDA, 2004). En effet, d'après Pankhurst et *al*. (1997), la santé du sol selon cette définition inclut le temps et reconnaît le sol comme "un système vivant essentiel", contrairement à la définition de la qualité du sol proposée par Doran et Parkin (1994).

La santé du sol étant définie, se pose la question de son estimation et de son suivi dans le temps, en particulier à l'égard des pratiques culturales, d'où la nécessité de développer des indicateurs de la santé des sols. Doran et Safley (1997) ont établi cinq critères que devraient posséder ces indicateurs: 1) être corrélés aux processus de l'écosystème; 2) intégrer les processus et les propriétés physiques, chimiques et biologiques du sol; 3) être suffisamment simples pour être utilisés par les spécialistes mais aussi par les producteurs agricoles; 4) être sensibles aux variations du climat et de l'utilisation du sol et à leurs effets à long terme sur les qualités du sol; 5) être des composants des bases de données de sol existantes, là ou c'est possible. Il apparaît évident que de tels critères sont difficiles, voire impossibles à satisfaire par un indicateur unique. Il convient donc d'utiliser une ou plusieurs séries d'indicateurs physiques, chimiques et biologiques qui auront chacun une fonction particulière dans l'évaluation de la santé du sol (Doran et Safley, 1997), ce qui rejoint la conception de Thaër précédemment exposée.

Doran et Zeiss (2000) proposent une synthèse des connaissances et opinions en santé des sols. On pourrait résumer leurs propos ainsi: la santé du sol promeut un environnement de qualité, et favorise entre autres la santé des plantes. En ce sens, la santé du sol est synonyme de durabilité ("sustainability") (Doran et Zeiss, 2000). Les indicateurs de santé du sol devraient: être sensibles aux perturbations d'origine anthropique de l'équilibre naturel d'un écosystème (agrosystème); être corrélés aux fonctions vitales ("beneficial") du sol; contribuer à comprendre et expliquer la dynamique et les processus des écosystèmes (ou des agrosystèmes) (Doran et Zeiss, 2000).

Les sections 2.1 à 2.3 présentent quelques indicateurs de la santé du sol. La stabilité structurale (Kemper et Rosenau, 1986) est le principal indicateur physique; son estimation et sa relation avec les pratiques culturales sont brièvement décrites (section 2.1). La dynamique de la matière organique (MO) (section 2.2) est un autre indicateur physico-chimique important, dans la mesure où cette dynamique est liée à la fois à la structure physique, à la composition chimique du sol, ainsi qu'à son activité biologique. La section 2.3 regroupe les indicateurs biologiques que sont les comptes bactériens, l'indice de fécondité du sol (Rusch, 1972) et le quotient de minéralisation du carbone (Dommergues, 1960).

2.1 La structure du sol: un indicateur physique de la santé des sols

Il existe de multiples définitions de la structure du sol. En anglais, Kay et Angers (1999) parlent du “tilth” qui décrit un état d’agrégation propice à la croissance végétale et caractérisé par un fractionnement régulier lors du travail mécanique, de la levée des plantules et de la croissance des racines, procurant ainsi un environnement optimal à la croissance des plantes et des micro-organismes. Rusch (1972) parle de “structure grumeleuse” qui fait référence à la présence de “grumeaux” ou de macroagrégats (>250μm).

2.1.1 Agrégation

La répartition et la résistance des zones de rupture vont conditionner, chez un sol donné, la répartition de la taille des agrégats en différentes classes. Les caractéristiques des zones de rupture sont principalement fonction de la texture du sol, de sa teneur en MO et de la composition des ciments qui lient les particules entre elles (organiques et inorganiques) (Kay et Angers, 1999).

Un agrégat est défini comme l'unité structurale issue de la fragmentation partielle du sol par l'humidification-dessiccation, le travail du sol ou tout autre perturbation physique. Les agrégats < 250 μm sont qualifiés de microagrégats alors que ceux > 250 μm sont qualifiés de macroagrégats en relation avec l'hypothèse hiérarchique de Tisdall et Oades (1982; cités par Kay et Angers, 1999) qui considèrent que les macroagrégats, dans la plupart des sols, sont formés d'agrégats < 250 μm. De plus, la nature des ciments est différente au sein de ces deux classes d'agrégats.

2.1.2 Dynamique de l'agrégation

Dans une étude des sols de la vallée du Saint-Laurent (loams limono-argileux), Angers (1998) rapporte qu'une proportion significative des variations à court terme (jours, semaines) de l'agrégation est due aux conditions climatiques et en particulier au contenu en eau des agrégats qui deviennent plus sujets à l'éclatement à mesure qu'ils sèchent. Angers (1998) observe également que l'effet du climat se fait moins sentir sous travail réduit ou sous couvert végétal plus constant (luzerne, graminées pérennes). La résistance à l'éclatement est liée à la sensibilité des sols à l'érosion et à la formation d'une croûte superficielle (Angers, 1998). La plupart des études sur les sols argileux de la vallée du Saint-Laurent montrent que la proportion de macroagrégats change rapidement (en quelques années) sous l'influence du travail du sol, des rotations et des amendements organiques (Angers, 1998).

2.1.2.1 Effets de la matière organique et des amendements

Dans la même étude, Angers (1998) montre que la proportion d'agrégats stables (> 1 mm) est linéairement corrélée aux intrants de C organique estimés sous diverses régies (plus de 2 ans): orge et trèfle/labour ou chisel/fertilisation minérale conventionnelle ou purin de bovins laitiers. Angers (1998) observe que les facteurs qui influencent le plus l'agrégation sont la plante cultivée suivie de la fertilisation par son apport de C. Dans un système plus complexe de rotations, il est difficile de corréler l'apport de C avec l'agrégation. Les effets directs des intrants de C sont plus clairement estimés lorsque la seule variable de l'étude est l'apport d'amendements organiques (Angers, 1998).

Aoyama et *al*. (1999) étudient l'effet à long terme (18 ans) de l'apport de fumier de bovin sur l'agrégation et la teneur en MO dans un loam de la vallée du Saint-Laurent. Le fumier augmente

significativement la proportion de la fraction la plus faible des macroagrégats (250-1000 μm) par rapport à la fertilisation minérale et au traitement témoin, tandis que la fertilisation minérale ne modifie pas l'agrégation par rapport au traitement témoin. Cette augmentation de la fraction la plus faible des macroagrégats est associée à une augmentation de la teneur en C des agrégats dans cette fraction en particulier. Selon Aoyama et *al*. (1999), la MO du fumier est incorporée au sol sous forme particulaire puis, sous l'action des micro-organismes, la MO est associée à la fraction minérale puis incorporée aux agrégats dont elle améliore la stabilité.

Au Québec, dans les loams limono-argileux, la réponse de la macroagrégation à l'application d'amendements divers serait corrélée positivement à leur dégradabilité. Par exemple, l'application de tourbe humifiée a montré un effet lent mais prolongé sur l'agrégation, tandis que l'application de tourbe fibreuse (plus décomposable) a eu un effet beaucoup plus marqué sur la résistance des agrégats à l'éclatement (Dinel et *al*., 1991; cités par Angers, 1998). L'application de boues de désencrage (BD) (dérivées du recyclage du papier) chez un loam argileux appuie cet énoncé. Ainsi, Chantigny et *al*. (1999) rapportent une forte augmentation de la macroagrégation dans les 370 jours qui suivent l'application des BD et ils attribuent cette agrégation à la décomposition rapide de la fraction cellulosique des boues qui produit des composés organiques liants par l'intermédiaire des micro-organismes (polysaccharides, lipides…). Trois ans après l'application de BD, l'agrégation est toujours significativement plus élevée dans les traitements ayant reçu les boues. Chantigny et *al*. (1999) attribuent cette persistance de l'agrégation à la fraction la moins décomposable des BD, fraction ligneuse ou protégée de la dégradation par l'incrustation dans l'argile. Une autre étude qui caractérise les effets de 9 ans d'application de résidus ligneux chez un loam sableux (N'Dayegamiye et Angers, 1993) montre que ces résidus faiblement décomposables n'induisent pas de changement significatif dans la proportion de macroagrégats stables mais plutôt un enrichissement en substances humiques du sol (agents stabilisants des microagrégats) ainsi qu'une augmentation du C total.

2.1.2.2 Effets des rotations

L'effet des plantes cultivées sur la structure et l'agrégation du sol varie considérablement d'une espèce à l'autre et même d'un cultivar à l'autre (Kay, 1990). Ces variations sont attribuées au développement du système radiculaire, à l'extraction de l'eau, à la quantité de photosynthétats libérés dans le sol et à leurs caractéristiques (Kay, 1990). Par exemple, la rhizodéposition du

brome (*Bromus inermis*) est deux fois plus élevée et persistante que celle du maïs (*Zea mays*) (Davenport et Thomas, 1988; Davenport et *al*., 1988; articles cités par Kay, 1990). Elustondo et *al*. (1990, cités par Angers, 1998) ont montré une plus forte macroagrégation sous cultures fourragères que sous monoculture de maïs chez des sols à haute teneur en argiles. Les études où l'influence des cultures sur la stabilité du sol de surface est indépendante du travail du sol et du contenu initial en C montrent une corrélation entre l'accroissement de la longueur des racines et de la stabilité des agrégats à l'eau (Kay, 1990).

Le choix des cultures à introduire dans les rotations devrait donc prendre en compte l'état d'agrégation du sol ainsi que l'impact potentiel des cultures disponibles. Un choix judicieux des rotations, par introduction notamment de plantes fourragères pérennes, permet de limiter ou d'éliminer les effets néfastes de la monoculture de maïs par exemple. L'effet des rotations sur l'agrégation est également dépendant du type de travail du sol (Kay, 1990).

2.1.3 Stabilité structurale

La stabilité structurale définit la capacité d'un sol à conserver sa forme structurale. La stabilité structurale est spécifique à chaque forme structurale et dépend essentiellement des propriétés physiques et biologiques du sol, ainsi que de la nature des forces appliquées. Les principaux facteurs qui agissent sur la stabilité structurale sont les cycles humidification-dessiccation, le travail du sol et le passage de la machinerie. La stabilité structurale d'un sol est généralement estimée par l'humidification des agrégats suivie de l'agitation dans l'eau, du tamisage ou de l'ultrasonication. Pour cette raison, la stabilité des agrégats est généralement considérée comme synonyme de stabilité structurale (Kay et Angers, 1999).

2.1.4 Stabilité des agrégats à l'eau

La stabilité des agrégats à l'eau est définie comme la capacité des agrégats à résister à l'humidification suivie d'une agitation mécanique dans l'eau. Cette propriété des agrégats est utilisée pour étudier le degré de cohésion des agrégats et la dynamique des liaisons entre particules de sol. La stabilité des agrégats diminue à mesure qu'augmente la vitesse d'imbibition et est liée à l'air piégé au sein des agrégats ainsi qu'à l'expansion des argiles. La mesure de la stabilité à l'eau qui utilise une imbibition rapide est particulièrement indiquée chez les sols dont la surface est généralement sèche et rapidement humidifiée par des pluies intenses ou l'irrigation. Dans les situations moins contrastées où les précipitations sont régulièrement réparties dans la

saison (ou pour les agrégats qui ne sont pas en surface), l'imbibition devrait être plus progressive. Les échantillons ne sont alors pas séchés et, dans ce cas, la teneur initiale en eau influence fortement la stabilité des agrégats (Kay et Angers, 1999).

2.1.5 Diamètre Moyen Pondéré (DMP), une mesure de la stabilité structurale

Les meilleures méthodes pour déterminer la stabilité ou la distribution de la taille des agrégats ont évolué en fonction de la standardisation des forces destructives appliquées et des efforts pour les rendre comparables à celles qui prévalent au champ. L'intensité de la dégradation est estimée par la proportion (en masse) des agrégats fragmentés en agrégats ou particules primaires inférieurs à une taille donnée. La plupart des travaux sur la stabilité des agrégats dans l'eau pour estimer l'état de la structure d'un sol utilisent la technique développée par Yoder (1936, cité par Kemper et Rosenau, 1986). Cette technique consiste à agiter une série de tamis de taille décroissante dans l'eau, puis à estimer la proportion des agrégats sur chacun des tamis. Comme les agrégats les plus gros sont plus indicatifs d'une meilleure structure que celle d'une quantité équivalente de petits agrégats, Van Bavel (1949, cité par Kemper et Rosenau, 1986) propose d'assigner un facteur de pesée proportionnel à la taille des agrégats. Le paramètre que Van Bavel qualifie de diamètre moyen pondéré (DMP) est égal à la somme des produits des diamètres moyens (x_i) et de la proportion du poids total de l'échantillon (w_i) de chacune des fractions de taille où $DMP = \Sigma\, x_i\, w_i$ (Kemper et Rosenau, 1986).

2.2. Dynamique de la matière organique

La mise en culture des sols couverts par la forêt ou les prairies natives conduit généralement à une diminution de leur contenu en C organique, de par le changement de végétation et la diminution des intrants de MO qui s'ensuivent (Kay et Angers, 1999). Angers et Carter (1996) rapportent que la diminution de la couverture du sol ainsi que le travail du sol augmentent la température du sol conduisant à une minéralisation du C libéré dans l'atmosphère sous forme de CO_2 (Davidson et Ackerman, 1993; Schlesinger, 1990; articles cités par Angers et Carter, 1996). Martel et Deschênes (1976; cités par Angers et Carter, 1996) rapportent une perte moyenne de 30 % du carbone (C) après 30 ans de mise en culture de trois sols forestiers du Québec. Les modifications structurales des sols associées à cette perte nette de C, qui se manifeste par la dégradation de l'agrégation, sont mal connues ainsi que les effets des pratiques culturales sur les stocks de C. S'impose donc une meilleure compréhension de la dynamique du C dans les sols

cultivés en fonction des pratiques culturales de façon à prévenir les effets néfastes de ces pratiques et à promouvoir des pratiques qui permettent de maintenir et d'augmenter le stock de C dans le sol (Kay et Angers, 1999).

2.2.1 Effets des amendements

L'application d'azote minéral peut à court terme accélérer la minéralisation du C organique (Acton et *al*., 1963; cités par Angers et Carter, 1996). Cependant, les effets directs à long terme sont généralement considérés comme négligeables (Angers et Carter, 1996). L'augmentation de la productivité végétale associée à la fertilisation azotée semble avoir un effet indirect positif sur le contenu du sol en C organique total (Angers et Carter, 1996). Plusieurs études montrent que l'apport d'azote sous forme minérale ou organique accélère la dégradation de composés organiques intervenant dans la formation d'agrégats (Elliott et Lynch, 1984; Harris et *al*., 1966; articles cités par Kay, 1990). Selon Kay (1990), la production accrue de tissus végétaux issue de la fertilisation azotée peut voir ses effets positifs annulés si elle induit une accélération de la minéralisation du C et ces effets seront accentués si elle induit également une diminution de la production de mucilage.

L'étude à long terme (18 ans) par Aoyama et *al*. (1999; cf. section 2.1.2.1) de l'application de fumier de bovin comparée à la fertilisation minérale montre que cette dernière n'a pas d'effet significatif sur la teneur en C et N total du sol, alors que le fumier entraîne une accumulation de C et N dans toutes les fractions du sol > 53 μm et en particulier les petits macroagrégats (250-1000 μm). Cette accumulation concerne le C "libre" (de la MO particulaire) et associé à la fraction minérale. On constate également une diminution du rapport C/N dans les macroagrégats > 1000 μm et dans la MO particulaire des macroagrégats 250-1000 μm (Aoyama et *al*., 1999). L'étude d'Aoyama et *al*. (1999) montre un effet faible ou nul de la fertilisation minérale sur les qualités du sol tandis que l'apport de fumier est associé à une amélioration de la structure du sol et à un stockage de nutriments dans le sol, excepté dans la fraction la plus fine (< 53 μm). Ces résultats suggèrent que cette fraction est saturée en MO (Angers, 1998), ou que l'application de fumier produit peu de MO récalcitrante (composés humiques) à long terme contrairement aux résidus de bois (N'Dayegamiye et Angers, 1993). L'application de boues de désencrage (BD) (Chantigny et *al*., 1999) montre une dynamique similaire après 3 ans. Les boues restent surtout sous forme particulaire > 53 μm et sont probablement minéralisées plutôt que de rejoindre la

fraction du C la plus fine (< 53 μm). On peut s'attendre à ce que les effets du fumier ou des BD sur la macroagrégation notamment disparaissent après quelques années suivant l'arrêt de leur application.

2.2.2 Effets des rotations

Les cultures fourragères pérennes sont actuellement les plus utilisées et les plus efficaces pour maintenir et augmenter la teneur du sol en C, comme elles le sont pour rétablir l'agrégation. En 2-3 ans, des changements sont mesurables dans la fraction labile du C (Angers et Carter, 1996). Angers (1992; cité par Angers et Carter, 1996) montre que le contenu en C organique d'une argile de Kamouraska (gleysol humique) augmente de 25 g kg^{-1} à 29 g kg^{-1} environ sous luzerne alors que dans le même temps, il diminue sous maïs et dans le traitement témoin sans couvert végétal. Il existe cependant peu de données sur la production et le devenir du C selon les cultures (Angers et Carter, 1996). Les connaissances font défaut également chez les principales cultures commerciales. Cependant, des modèles prédictifs suggèrent que des intrants de 2-3 Mg C ha^{-1} seraient suffisants pour maintenir la teneur du C à 20 g C kg^{-1} (Voroney et Angers, 1994; cités par Angers et Carter, 1996). Mis à part la pomme de terre (*Solanum tuberosum* L.), le maïs d'ensilage et le soja qui produisent moins de 1 Mg C ha^{-1}, la plupart des cultures des climats tempérés produisent plus de 2 Mg C ha^{-1} et seraient ainsi capables de maintenir la teneur du C du sol (Bolinder et Angers, 1993; Carter et *al*., 1989; articles cités par Angers et Carter, 1996).

2.2.3 Limites du modèle physique

Les études citées par Kay et Angers (1999) montrent le rôle prépondérant que jouent l'agrégation et la stabilité des agrégats pour conserver une structure capable de soutenir une productivité intensive. La dynamique de l'agrégation est étroitement dépendante du C organique du sol, en particulier la macroagrégation, dont la stabilité dépend de la fraction labile du C et de l'activité des micro-organismes du sol. Le modèle théorique qui sous-tend ces recherches est le modèle hiérarchique proposé par Edwards et Bremner (1967). Ce modèle suggère que les unités élémentaires de la structure du sol sont les microagrégats stables (< 250 μm) dont la cohésion est assurée par des composés organiques relativement instables et les êtres vivants. Les microagrégats s'associent entre eux pour former des macroagrégats. Angers (1998) utilise ce modèle pour expliquer la réponse rapide des sols du Québec (vallée du Saint-Laurent) aux pratiques de conservation. Ces sols seraient caractérisés par une microagrégation extrêmement stable parce que saturée en MO. Tout apport de MO ou toute pratique de conservation

entraînerait une macroagrégation rapide et une accumulation de MO particulaire. Selon ce modèle, plus le déficit en MO croît, plus il va affecter la MO stable et ancienne des substances humiques résultant de siècles et peut-être de millénaires d'accumulation dans les écosystèmes natifs. Même si ces fractions anciennes de la MO n'influencent pas directement la croissance des plantes et la productivité, leur perte pourrait s'avérer très dommageable (Kay et Angers, 1999). Enfin, la structure exerce un effet dominant sur l'activité microbienne du sol car elle influence fortement la disponibilité des nutriments. Par l'intermédiaire des micro-organismes, cet effet s'étend donc au cycle du C et des nutriments. De par son hétérogénéité spatiale, le sol favorise le développement d'une flore microbienne diversifiée capable de se développer sur les résidus organiques de toute nature, assurant ainsi la libération des éléments complexés de la MO. Or, selon Kay et Angers (1999), il n'existe pas à ce jour de modèle général qui explique cette dynamique.

2.3 Les micro-organismes: indicateurs biologiques de la santé des sols

Les micro-organismes ont la particularité de donner une mesure intégrée de la santé du sol qui ne peut être obtenue par les mesures de physico-chimie ou des organismes multicellulaires. Les micro-organismes sont également susceptibles de répondre plus rapidement aux changements de la santé du sol en raison de leur contact plus intime avec le sol. En effet, leur rapport surface/volume élevé confère aux micro-organismes une plus grande surface d'échange avec le sol (Nielsen et Winding, 2002). Selon Rapport et *al*. (1997), l'état actuel des connaissances ne permet pas de recommander les indicateurs biologiques comme des outils de routine pour évaluer la santé du sol. Or, cet avis n'est pas partagé par tous les auteurs. En effet, Nielsen et Winding (2002) déplorent pour leur part que les indicateurs microbiologiques ne soient que peu représentés dans les programmes officiels de suivi de la santé des sols. Nielsen et Winding (2002) insistent notamment sur le fait que ces indicateurs biologiques doivent être accompagnés d'indicateurs physico-chimiques essentiels à l'interprétation des données et variables biologiques. Nielsen et Winding (2002) insistent également sur la pertinence d'utiliser la présence d'organismes pathogènes comme indicateurs de santé du sol, au même titre que la présence des organismes bénéfiques. En effet, la présence de maladies des racines (Hornby et Bateman, 1997) ou des maladies des plantes en général est de longue date considérée comme un précieux indicateur de déséquilibre au sein des sols et des écosystèmes/agrosystèmes (Howard, 1971; Rusch, 1972). La notion de sol suppressif (Alabouvette, 1999) illustre le potentiel des agents

pathogènes comme indicateurs de la santé des sols. En effet, ces sols suppressifs sont capables de contrer le développement d'une maladie naturellement, ou suite à des pratiques culturales particulières (Bailey et Lazarovits, 2003; Lazarovits, 2001; Weller et *al*., 2002).

2.3.1 Les comptages directs

Les méthodes directes d'estimation de l'abondance microbienne par comptages directs des cellules, après coloration (Schmidt et Paul, 1982), après coloration et fixation (Riis et *al*., 1998; Schmidt et Paul, 1982) ou sans coloration ni fixation (Rusch, 1972), requièrent beaucoup de temps et de pratique, mais elles donnent les résultats les plus représentatifs des conditions du sol in situ, et par conséquent sont encore fréquemment utilisées (Bloem et Breure, 2002). De plus, ces méthodes permettent de traiter de nombreux échantillons d'origines différentes, alors que les méthodes indirectes qui estiment la biomasse microbienne, bien que plus faciles d'utilisation, ne donnent pas forcément des résultats comparables d'un sol à l'autre (Anderson et Domsch, 1978). Par exemple, la controverse concernant les constantes utilisées pour convertir le C du CO_2 respiré après fumigation en biomasse microbienne se poursuit (Jenkinson et *al*., 2004).

2.3.2 Un indice de fécondité du sol

Un indice de santé des sols consiste en l'intégration de plusieurs indicateurs (microbiens) de la santé des sols dans une seule valeur, en pondérant chacune des mesures les unes par rapport aux autres. Des seuils peuvent être établis par la suite pour créer une échelle (Nielsen et Winding, 2002). Le principal problème lié aux indices est la perte d'information liée aux relations entre chacun des indices séparés et le caractère subjectif de la pondération (Stenberg, 1999). Rusch (1972) a proposé un indice de fécondité du sol basé sur les Lactobacteriaceae (Eubactéries). Ce groupe de bactéries lactiques s’est révélé systématiquement associé aux racines de plusieurs espèces de plantes et à tous les sols testés par Rusch (1972). Dans des sols stérilisés avant les semis et arrosés avec de l’eau de pluie, les bactéries lactiques sont les premières à coloniser les racines, selon Rusch (1972). Ces bactéries sont des symbiotes non obligatoires de la rhizosphère et seraient des intermédiaires importants entre les plantes et la MO. Ainsi leur présence et leur état physiologique seraient liés à la fécondité du sol selon Rusch (1972). L'expression "fécondité du sol" est utilisée à dessein car elle fait référence à la capacité continue des organismes qui vivent du sol à se reproduire. Cette expression est une référence directe à "l'échelle de fécondité du sol" de Thaër (cité par Feller et *al*., 2003) et correspond au caractère holistique donné à la

récente définition de la santé du sol par Doran et Safley (1997) et Doran et Zeiss (2000). Cependant, la comparaison de l'indice de Rusch (1972) à des méthodes officielles d'estimation de la biomasse et de l'activité biologique des sols de trois systèmes culturaux (conventionnel, bio-Dynamique, bio-Organique) n'a pas permis de corréler cet indice avec les méthodes officielles (Mäder et *al*., 1993). Cette étude comparative de Mäder et *al*. (1993) est à ce jour la seule publiée sur l'indice de fécondité de Rusch (1972). Ce manque d'intérêt peut s'expliquer par le fait que cet indice ait été développé pour l'agriculture biologique. De plus, les bactéries lactiques, dont font partie les coliformes de type *Escherichia coli*, sont surtout considérées comme potentiellement pathogènes chez l'humain et leur présence est strictement contrôlée dans l'eau ou les composts, par exemple (CAN/BNQ, 1996). Cependant, à part quelques rares exceptions, ces bactéries ne sont pas pathogènes et sont présentes naturellement dans la plupart des milieux terrestres et aquatiques (Atlas et Bartha, 1998). Ces constatations ont notamment conduit à la remise en question des normes pour les composts et les résidus organiques comme les boues de papetières (F. Gauthier, comm. pers.). De plus, des techniques d'étude directe de l'activité métabolique au sein de la rhizosphère à l'aide de biosenseurs utilisent le symbiote des racines *Erwinia herbicola* souche 299R, une Lactobacteriaceae proche de *E.coli*, comme organisme test (Farrar et *al*., 2003). Ces nouveaux développements pourraient contribuer à renouveler l'intérêt pour l'indice de fécondité développé par Rusch (1972) et pour la théorie qui le sous-tend (Rusch, 1950) comme c'est le cas pour les travaux de Thaër (Feller et *al*., 2003).

2.3.3 La respiration du sol

La respiration du sol, qui est l'oxydation biologique de la MO en CO_2 par les organismes aérobies, occupe une position déterminante dans le cycle du C au sein des écosystèmes terrestres. L'activité métabolique des organismes du sol peut être estimée par le dégagement de CO_2 ou la consommation d'oxygène. La mesure de l'activité respiratoire du sol est une des plus anciennes techniques d'évaluation de l'activité microbienne, et encore l'une des plus utilisées à ce jour (Nielsen et Winding, 2002). Comme la respiration du sol est très sensible à la température, l'humidité du sol, la disponibilité des nutriments et la structure du sol, la standardisation des conditions d'incubation au laboratoire est essentielle pour que la mesure de l'activité respiratoire soit un indicateur rigoureux de la qualité de la MO et des processus de décomposition (Sparling, 1997). Le quotient métabolique (qCO_2) est défini comme le rapport du C du CO_2 sur le C de la biomasse microbienne déterminé par la méthode de la respiration induite d'un substrat (substrate

induced respiration: Anderson et Domsch, 1990). C'est l'une des méthodes les plus utilisées pour la mesure de l'activité métabolique des micro-organismes du sol. Le qCO_2 est généralement plus élevé lorsque la pression exercée sur l'écosystème est forte, ou lorsque l'écosystème est moins mature d'après la "théorie énergétique" de Odum (1969; Maire et *al*., 1999), théorie énergétique judicieusement reprise et expliquée par Anderson (2003). Le quotient de minéralisation du carbone (QMC) a été défini par Dommergues (1960) et développé notamment par Bachelier (1968) pour caractériser des types pédologiques en fonction de leur activité biologique. La technique consiste à estimer le dégagement de CO_2 d'un sol pendant un temps donné et à exprimer le C minéralisé sous forme de CO_2 par rapport au C organique du sol: QMC = C du CO_2/C organique du sol * 100. On peut par la suite comparer les sols en fonction du QMC pour une durée déterminée, ou en fonction de la dynamique du QMC pendant toute la durée de l'incubation.

Dans la section 2.3.4, on s'attarde plus précisément aux relations entre les agents pathogènes telluriques et les propriétés du sol. Y sont présentés notamment quelques effets des pratiques culturales, dont les sols suppressifs, et le cas de maladies à *Sclerotinia*.

2.3.4. Les agents pathogènes du sol

Le développement de maladies telluriques a occasionnellement été associé à une diminution de la santé des sols ("Soil health": Hornby et Bateman, 1997; Howard, 1971; Rusch, 1972). Quelques articles de synthèse intègrent la santé des sols et la phytopathologie (Abawi et Widmer, 2000; Pankhurst et *al*., 2003; Sturz et Christie, 2003; van Bruggen et Semenov, 2000), ces thèmes étant inter-reliés dans des recherches appliquées, par exemple au Canada (Carter et *al*., 2003). Ces constatations sont à l'origine de l'étude des agents pathogènes comme indicateurs potentiels de la dégradation de la santé des sols.

2.3.4.1 Relations entre les agents pathogènes et la structure du sol

La dégradation de la structure du sol peut entraîner des problèmes de croissance et des pertes de rendements des cultures. La compaction par le passage de machinerie lourde est aggravée par la diminution de la stabilité structurale et entraîne des problèmes de drainage, d'aération qui, même en absence d'agent pathogène, entravent la croissance des racines et perturbent le développement

de la rhizosphère. Ces perturbations favorisent le développement de maladies radiculaires comme le piétin échaudage des céréales causé par le *Gaeumannomyces graminis* Sacc. (Hornby and Bateman, 1997). Chez le pois (*Pisum sativum* L.), l'oomycète pathogène des racines, *Aphanomyces euteiches* Drechs., occasionne des pertes graves dans les sols mal drainés et compactés par la machinerie lourde. L'enfouissement d'avoine (*Avena sativa* L.) ou de pois en préculture contribue à réprimer la pourriture à *Aphanomyces* chez le pois. L'amélioration de la structure du sol par l'amendement de MO fraîche améliore le drainage et crée des conditions défavorables à l'infection du pois par l'*A. euteiches*. Si la structure est à nouveau perturbée par une circulation excessive de la machinerie, les effets suppressifs sur la pourriture du pois disparaissent (Allmaras et *al*., 2003).

Il existe des cas particuliers où une meilleure stabilité structurale (plus forte proportion d'agrégats > 200 μm) est associée à un développement accru de la maladie, tel le cas de la fusariose du bananier causée par le *Fusarium oxysporum* (Schlect.) f. sp. *cubense*. Dominguez et *al*. (2001) attribuent ce phénomène à une meilleure disponibilité du fer créée par l'anoxie à l'intérieur des macroagrégats. Le fer est un élément essentiel à la germination des spores du *F. oxysporum* et on observe des carences en fer dans la solution des sols suppressifs pour cet agent pathogène. En effet, de tels sols suppressifs ont une plus faible proportion de macroagrégats que des sols non suppressifs, donc moins d'anoxie, l'anoxie étant essentielle aux processus chimiques et biologiques qui conduisent à la solubilisation du fer (Dominguez et *al*., 2001).

2.3.4.2 Effets du travail du sol sur les pourritures à Sclerotinia

D'une part, le labour a été recommandé en association avec un fongicide chez le pois et la laitue (*Lactuca sativa*) pour réduire la gravité de la sclérotiniose (Merriman et *al.*, 1979). D'autre part, la réduction de la sclérotiniose, attribuée à une baisse de fructification des sclérotes, ne s'est pas confirmée au-delà de la première année lorsque le labour était utilisé chez le canola (*Brassica* spp.) (Williams et Stelfox, 1980). De même, Cook et *al.* (1975) n'observaient aucune réduction de la gravité de la sclérotiniose chez le pois après un labour profond. Bailey (1996) précise que les résidus de culture non-hôte laissés en surface par le non travail du sol réduisent la gravité de la sclérotiniose en augmentant l'humidité du sol et l'activité biologique en surface, participant ainsi à la dégradation plus rapide des sclérotes. Ces observations concordent avec celles de Workneh et Yang (2000) qui constatent, sur une période de 4 ans, une intensité moindre de la sclérotiniose lorsque le sol n'est pas travaillé par rapport au travail conventionnel (labour).

Workneh et Yang (2000) attribuent cet effet à un couvert végétal moins dense et une plus forte agrégation des sclérotes en semis direct. En revanche, Workneh et Yang (2000) constatent que le travail conventionnel (labour) est plus efficace que le travail réduit pour contrer la sclérotiniose. Kurle et *al*. (2001) constatent également que le non travail du sol génère les meilleurs rendements en soja devant le chisel et le labour et ce, à deux stations caractérisées respectivement par une faible incidence de la sclérotiniose (< 1 %) et une forte incidence (> 40 %). La faible survie des sclérotes en surface a été rapportée par Maheu (1999) à Saint-Hyacinthe (Québec, Canada): les parcelles labourées portaient plus de sclérotes viables ou de nouveaux sclérotes que les parcelles de soja en travail réduit. Ces quelques recherches appuient la restriction du labour dans les champs de soja affectés par la sclérotinose au Québec pour limiter l'accumulation de sclérotes en dormance dans le sol.

2.3.4.3. Relations avec les rotations

Effet des rotations sur les agents pathogènes du sol

Bailey et *al*. (2001) rapportent des effets limités des rotations sur la gravité des maladies foliaires et radiculaires des céréales, ainsi que sur la structure des populations d'agents pathogènes. Or, Bailey et *al*. (2001) constatent une diminution de l'incidence des maladies foliaires du blé lorsque celui-ci est cultivé après une jachère ou une culture de pois, plutôt qu'après le blé. De plus, même si les rotations ne réduisent pas la gravité ou l'incidence des maladies, les rendements du blé sont habituellement plus élevés lorsqu'il est cultivé en rotation avec le pois, le lin ou d'autres céréales, que s'il est cultivé en monoculture. De plus, sans réduire les maladies, les rotations réduisent les populations de la plupart des agents pathogènes du sol, sauf les *Fusarium* spp. dont les populations peuvent augmenter lorsque le lin est inclus dans la rotation.

La rotation est un moyen agronomique, économique et efficace pour lutter contre les agents pathogènes du sol (Krupinsky et *al*., 2002). Il convient cependant de bien connaître les effets des rotations sur les divers agents pathogènes pour planifier efficacement la succession des cultures et intégrer d'autres moyens de lutte pour compléter les lacunes éventuelles des rotations. Par exemple, dans le cas de l'agent pathogène *Pyrenophora tritici-repentis* (Died.) Drechs. chez le blé, une rotation de 1-2 ans réduit significativement la charge d'inoculum et l'incidence de la tache foliaire lors du retour de la culture du blé. Dans le cas de l'agent de la jambe noire du canola, le *Leptosphaeria maculans* (Desmaz.) Ces. & De Not., plus de spores sont produites sur

des résidus de canola âgés de 2-3 ans que sur des résidus vieux d'un an seulement. Une courte rotation d'une saison seulement s'imposerait dans ce cas. Dans d'autres cas comme celui des agents pathogènes *Fusarium* spp., *Pythium* spp. et *Sclerotinia* spp., les rotations peuvent s'avérer peu efficaces, voire inefficaces ou même aggraver la situation notamment à cause de la large gamme d'hôtes de ces champignons qui limite le choix des cultures de rotation ou permet leur développement chez les adventices. Il convient donc, dans ces cas difficiles, d'associer d'autres moyens de lutte à la rotation comme le travail du sol, l'usage de fongicides, d'agents de lutte biologique ou des amendements organiques (Krupinsky et *al*., 2002).

Effet des rotations sur les pourritures à *Sclerotinia*

La rotation avec une culture non-hôte comme le maïs (*Zea mays*) et les céréales est un moyen préconisé pour diminuer la quantité de sclérotes du *S. sclerotiorum* (Mitchell et Wheeler, 1990; Rahe et Utkhede, 1985). La fructification sous espèce non-hôte serait équivalente à celle sous culture sensible (Schwartz et Steadman, 1978; Williams et Stelfox, 1980). De plus, les sclérotes qui ont fructifié s'épuisent et meurent (Mitchell et Wheeler, 1990). À Saint-Hyacinthe, en absence de germination carpogénique, le degré de dégradation des sclérotes s'est révélé équivalent quelle que soit la culture (maïs, céréales, soja) (Maheu, 1999). Les rotations seules se révèlent insuffisantes à éradiquer l'inoculum sur une période de 3 ans. Les sclérotes résiduels occasionnent une faible épidémie chez le pois et initient un nouveau cycle d'accumulation de sclérotes (Schwartz et Steadman, 1978). On rapporte également un nombre constant de sclérotes résiduels sous diverses rotations d'espèces non-hôtes (Steadman, 1979). On souligne encore un nombre constant d'apothécies produites par saison avant ou après 2 ans de culture d'orge (*Hordeum vulgare*) (Williams et Stelfox, 1980). Comme le suggèrent Alexander et Stewart (1994), un faible nombre de sclérotes persistants constitue la part réellement active de l'inoculum. Kurle et *al*. (2001) ont rapporté, à deux stations d'étude caractérisées par des incidences très différentes de sclérotiniose (< 1 % et > 40 %), que les rendements du soja étaient toujours meilleurs après la culture d'une espèce non-hôte (maïs ou avoine), mais que les meilleurs rendements étaient obtenus lorsque l'introduction d'une espèce non-hôte dans la rotation était associée au semis direct. Dans une étude similaire, Garcia-Garza et *al*. (2002) aboutissent aux mêmes conclusions et montrent que la production d'apothécies, inoculum primaire du *S. sclerotiorum*, est d'avantage réduite par la combinaison rotation-semis direct que par ces pratiques individuelles.

Hao et *al*. (2003) rapportent que la monoculture de laitue (pendant 3 ans) n'entraîne pas d'augmentation significative de l'intensité de la sclérotiniose dans les champs à faible densité d'inoculum (sclérotes de *S. minor*). Hao et *al*. (2003) notent cependant une diminution de l'inoculum dans le sol et de la gravité de la sclérotiniose par l'alternance des cultures de laitue et de brocoli (*Brassica oleracea* L. var. *botrytis* L.) lorsque les résidus du brocoli sont incorporés au sol après récolte, confirmant ainsi le potentiel de répression de la sclérotiniose par l'utilisation de certaines cultures en rotation.

Dans le cas du maïs, la culture non-hôte la plus rentable et la plus souvent choisie au Québec en rotation avec le soja, Maheu (1999) a montré à Saint-Hyacinthe chez un loam sableux, entre 1997 et 1998, que la dégradation des sclérotes est équivalente en culture de maïs et de soja, que la fertilisation soit minérale ou organique (purin de porc). Ainsi, la rotation seule ne s'avérait que partiellement efficace à contrer les épidémies, et la rotation devrait être associée au travail réduit ou à l'apport d'amendements organiques, façons culturales prometteuses, pour réprimer la sclérotiniose.

2.3.4.4. Relations avec les amendements organiques

Effets suppressifs

Hornby (1983) évoque ainsi le caractère "suppressif" ("suppressiveness") d'un sol. Dans un sol, ..."la suppression de la maladie ("disease suppression") s'exprime lorsque l'intensité de la maladie est moindre que prévue en présence d'un hôte sensible, d'un agent virulent, et sous des conditions normalement favorables ou "réceptives" ("conducive") à l'infection". En revanche, par favorable ("conducive soil") ou réceptif ("soil receptivity"), Alabouvette (1986) entend la capacité d'un sol à favoriser ou promouvoir l'établissement, le développement, la persistance et l'expression du pouvoir pathogène d'un agent pathogène chez son hôte. Quelques recherches illustrent le dynamisme des chercheurs internationaux (Abadie et *al*., 1998; Alabouvette, 1999; Cook et Baker, 1983; Garbeva et *al*., 2004; Mazzola, 2004; Postma et *al*., 2003; Stone et *al*., 2001; Weller et *al*., 2002) ou canadiens (Bailey et Lazarovits, 2003; Lazarovits, 2001; Martinez et *al*., 2002; Peters et *al*., 2003) sur les sols suppressifs.

L'interdiction d'un biocide utilisé pour la fumigation des sols en plein champ (bromure de méthyl), il y a maintenant 12 ans au Canada, a stimulé le développement de la recherche de

moyens de lutte autres que chimiques contre les agents pathogènes du sol et sur l'explication des effets suppressifs des sols (Lazarovits, 2001). Ces phénomènes suppressifs sont très divers et souvent associés à une culture ou à un type de sol particuliers.

D'une manière générale, on attribue les effets suppressifs des sols à des facteurs physiques, chimiques (Dominguez et *al*., 2001; Lazarovits, 2001) ou biochimiques (Morra et Kirkegaard, 2002), ou encore microbiologiques ou enzymatiques (Rasmussen et *al*., 2002). Les effets microbiologiques peuvent être liés à l'activité biologique globale du sol (Pankhurst et *al*., 2002), la diversité microbienne (van Elsas et *al*., 2002), la compétition pour les nutriments ou pour une niche écologique, dans la rhizosphère en particulier (Raj et *al*., 2003). On étudie également les effets antagonistes d'espèces ou de souches particulières, ainsi que de souches sélectionnées pour la production accrue d'antibiotiques (Dhingra et *al*., 2003; Knox et *al*., 2000). L'utilisation de la lutte biologique est l'avenue la plus étudiée pour lutter contre les agents pathogènes du sol en absence de moyen chimique ou de résistance génétique de la plante hôte. Cependant, les moyens biologiques sont loin d'avoir produit les résultats escomptés au champ malgré les promesses des expériences en conditions contrôlées. La prise en compte de la complexité des interactions encore mal connues au sein du sol et de la rhizosphère a sans doute été négligée. Les chercheurs tentent donc actuellement de favoriser l'établissement des agents de lutte biologique ainsi que leur efficacité dans le temps. Pour ce faire, il importe de bien comprendre les interactions de ces micro-organismes antagonistes avec le milieu où ils évoluent et avec les agents pathogènes qu'ils sont censés réprimer. Toute tentative de compréhension des interactions présentes au sein de l'écosystème que l'on tente de modifier devrait être un préalable systématique à toute introduction d'agents de lutte biologique (Knox et *al*., 2000). En effet, négliger la complexité des interactions qui participent à l'équilibre d'un écosystème conduit souvent à l'échec des tentatives de créer un effet suppressif. Gamliel et *al*. (2000) montrent comment l'apport raisonné de MO au sol peut favoriser l'installation d'une microflore bénéfique et suppressive aux agents pathogènes telluriques après un traitement intense du sol par la chaleur (solarisation), traitement qui s'apparente à une fumigation dans ses effets sur la microflore.

Effets suppressifs des amendements organiques et des composts

L'utilisation des amendements organiques pour réprimer les maladies telluriques est d'actualité. Discrédités par manque de reproductibilité des résultats, on tente actuellement de mieux comprendre les modes d'action des amendements organiques afin de choisir adéquatement les

matériaux et les procédés les plus efficaces pour produire les effets suppressifs escomptés (Lazarovits, 2001). Comme dans le cas des sols suppressifs, les processus impliqués par les amendements organiques sont complexes et variés. Lazarovits (2001) a pu identifier plusieurs modes d'action chez les amendements organiques généralement disponibles au Canada. Les amendements organiques riches en N, tels le fumier de volaille, les farines de viande ou d'os, les tourteaux de soja, réduisent significativement les populations de plusieurs agents pathogènes du sol [*Verticillium dahliae* (Kleb.), *Streptomyces scabies* (Thaxter), *F. oxysporum* f. sp. *lycopersici*, *S. sclerotiorum*]. Il a été démontré que l'ammoniac ou l'acide nitreux générés par la décomposition de ces amendements dans le sol sont responsables des effets suppressifs. Les teneurs de ces substances et composés dans le sol sont contrôlées principalement par le pH, la teneur en MO du sol, le pouvoir tampon et le taux de nitrification. Le fumier de porc, autre amendement riche en N mais aussi en phosphore, montre également des effets suppressifs lors de son application au sol, par la production d'ammoniac et d'acide nitreux, mais aussi d'acides gras volatiles actifs à pH < 6,0. D'autres amendements comme le lignosulfate d'ammonium, un sous-produit de l'industrie papetière, a montré un effet suppressif très marqué contre le *S. scabies*, procaryote pathogène reconnu chez la pomme de terre (*S. tuberosum*). Or, le mode d'action de cet amendement reste inconnu. Lazarovits (2001) a cependant montré que les populations bactériennes et fongiques des sols amendés une seule fois avec du lignosulfate d'ammonium augmentaient fortement et, même si les populations bactériennes revenaient à leur niveau initial après la première saison, les populations fongiques étaient encore 10 fois plus denses dans les sols amendés par rapport au traitement témoin, et ce après 3 ans.

D'une manière générale, l'application des amendements organiques peut se traduire par une augmentation d'un facteur 1000 des populations de micro-organismes telluriques. Lazarovits (2001) suggère que les processus de décomposition des amendements organiques et leurs sous-produits jouent un rôle prépondérant dans les phénomènes de suppression. A priori, le compostage au sol serait donc préférable à l'apport de compost à divers degrés de maturité pour des raisons évidentes de commodité. Or, d'autres études montrent que le compost offre un potentiel suppressif intéressant qui peut être supérieur à celui de ses matières premières. Par exemple, Coventry et *al*. (2002) montrent, dans des essais en serre, que le compost de déchets d'oignons est plus efficace que les déchets d'oignons non compostés à réprimer le champignon pathogène *Sclerotium cepivorum* Berk. chez l'ail (*Allium cepa* L.). Reuveni et *al*. (2002) montrent également des effets suppressifs très marqués d'un compost de fumiers (bovin et poulet) et de

paille de blé contre le *F. oxysporum* f. sp. *basilici* en serre. En plus de ces effets suppressifs, le compost stimule plus le développement du basilic (*Ocimum basilicum* L.) que la fertilisation minérale en présence ou en absence de l'agent pathogène. Cotxarrera et *al*. (2002) ont pu mettre en évidence l'effet suppressif de deux antagonistes du *F. oxysporum* f. sp. *lycopersici*, responsable de la fusariose de la tomate: le *Trichoderma asperellum* isolé d'un compost commercial et le *F. oxysporum* souche Fo47, une souche non virulente isolée d'un sol naturellement suppressif du *Fusarium* de la tomate. La souche Fo47 se montrait plus suppressive que le *T. asperellum* dans les essais en serre. Dans des essais sur un vert de golf, Boulter et *al*. (2002) montrent les effets suppressifs de deux composts contre deux agents pathogènes de l'agrostide (*Agrostis palustris*): les *Microdochium nivale* et *Typhula ishikariensis*. En plus de l'effet suppressif comparable à l'effet du traitement fongicide, les composts stimulaient le reverdissement de la graminée suite à l'effet des agents pathogènes ou de l'hiver, ce qui montre une fois encore le potentiel des composts à atténuer des problèmes liés aux agents pathogènes du sol.

Il est connu de longue date que l'apport de MO fraîche au sol a des effets potentiellement phytotoxiques, comme le souligne Lazarovits (2001). Par conséquent, il est recommandé d'appliquer ces amendements à l'automne qui précède la culture, ou suffisamment tôt avant le semis pour éviter ces effets phytotoxiques. Se pose alors le problème de la perte de l'effet suppressif si les processus de décomposition sont trop avancés au moment où les populations d'agents pathogènes se développent. Il convient donc de bien connaître les conditions qui prévalent dans les champs où on envisage d'appliquer des amendements de manière à obtenir l'effet suppressif escompté avec un maximum d'efficacité.

Suppression de pourritures à *Sclerotinia*

Asirifi et *al.* (1994) rapportent que chez la laitue, en Australie, la sclérotiniose est devenue un problème grave suite à la substitution des fumiers de bovins par les fertilisants chimiques. Ces chercheurs ont montré que les amendements organiques réduisent significativement la sclérotiniose de la laitue et la survie des sclérotes du *S. sclerotiorum* par rapport au traitement témoin sans amendement organique. Cet effet suppressif est attribué à la stimulation de la microflore tellurique. De plus, l'inhibition de la germination des sclérotes par les lessivats des amendements organiques suggère l'implication de toxines ou d'antibiotiques. Nakasone et *al.* (1999) ont mis en évidence, in vitro, l'inhibition significative de la croissance mycélienne du *S.*

sclerotiorum par des extraits aqueux de compost et de vermicompost. Seuls les extraits non autoclavés possédaient des effets inhibiteurs, ce qui suppose l'implication de micro-organismes ou de molécules biologiquement actives dans le(s) mécanisme(s) d'inhibition. Viana et *al.* (2000) concluent, eux aussi, que les amendements organiques constituent une approche viable pour la répression du *S. sclerotiorum*. En effet, Viana et *al*. (2000) notent, lors d'essais en serre, un effet suppressif significatif du lisier de porc sur la sclérotiniose du pois, le purin montrant plus d'efficacité qu'une suspension de *Bacillus subtilis* et qu'un traitement fongicide (iprodione). Boulter et *al*. (2000) rapportent que les effets suppressifs des composts envers les ravageurs des gazons (*S. homeocarpa* notamment) seraient dus à la fraction active de la microflore mésophile qui agirait par l'intermédiaire d'un ou d'une combinaison des facteurs suivants: compétition pour les nutriments, antibiose, enzymes lytiques extracellulaires ou autres enzymes extracellulaires, parasitisme, prédation ou enfin induction de la résistance de la plante hôte. Cependant, aucune des études citées par les auteurs qui précèdent ne précise la nature exacte des phénomènes conduisant à la suppression des maladies par les composts bien que plusieurs soulignent leur efficacité et leur intérêt économique.

Chez la laitue infectée par le *S. minor*, longtemps confondu avec le *S. sclerotiorum* (Wong et Willetts, 1975), l'application de composts de boues d'épuration pendant 4 ans réduit significativement l'intensité de la sclérotiniose (Lumsden et *al.*, 1986). Lumsden et *al.* (1986) attribuent cette répression à l'amélioration de la structure du sol, à la modification de son contenu en nutriments (N total, P, Ca, MO) et à l'augmentation de l'activité biologique estimée par l'activité déshydrogénase. D'autres études citées par Lumsden et *al.* (1986) rapportent les effets suppressifs des composts de boues d'épuration ou d'écorces sur le *S. minor* et sur d'autres agents pathogènes du sol (Hoitink, 1980). Kokalis-Burelle et Rodriguez-Kabana (1994) ont observé, in vitro, l'inhibition de la croissance mycélienne du *S. sclerotiorum* par de la poudre d'écorce de pin (*Pinus elliottii, Pinus taeda*) incorporée fraîche ou compostée au milieu de culture. La même préparation stimulait par ailleurs la croissance du *Penicillium citrinum*, champignon saprophyte non pathogène. Ces résultats appuient l'hypothèse selon laquelle l'absence de la sclérotiniose dans les sols biologiquement actifs serait liée à la compétition des micro-organismes saprophytes avec le *S. sclerotiorum*.

Une étude comparative de plusieurs sols rendus suppressifs à la sclérotiniose de la laitue (*S. sclerotiorum*) par des traitements à base de micro-organismes spécifiques pendant 6 ans attribue

l'effet suppressif des sols à l'amélioration de leurs propriétés physico-chimiques: élimination de la croûte de surface, augmentation de la taille des agrégats et un meilleur drainage (Tokeshi et *al.*, 1997). L'amélioration générale de ces propriétés affecterait la survie des sclérotes, d'une part par l'amélioration du drainage asséchant plus rapidement le sol en surface et d'autre part, par la stimulation de la microflore tellurique en général et, le cas échéant, des micro-organismes introduits pour lutter spécifiquement contre le *S. sclerotiorum*. Ces améliorations sont comparables, selon Tokeshi et *al.*(1997), à celles obtenues en agriculture biologique ou par le travail réduit.

Au contraire des études précédentes, Ferraz et *al.* (1999) montrent que l'augmentation de la teneur en MO du sol suite à l'incorporation de composts entraîne une incidence accrue de la sclérotiniose du pois. Cependant, cette augmentation est expliquée par une humidité plus favorable à la germination des sclérotes, humidité accrue associée à la MO et à la densité du couvert végétal. Bien que la plupart des études précédentes rapportent les effets suppressifs de l'apport de MO au sol sur la sclérotiniose, ces effets dépendent des conditions particulières du sol et de la culture.

3. Analyses multivariables et approche écosystémique en agronomie

3.1 Introduction à l'analyse multivariable ou multidimensionnelle

L'analyse multivariable ou multidimentionnelle regroupe un ensemble de méthodes numériques d'analyse qui traitent des matrices (tableaux) de données où chaque observation ou échantillon est défini par plusieurs variables, par exemple: des abondances d'espèces, des données de gravité de maladie... Ces analyses de données sont principalement dérivées de l'écologie numérique, une branche de l'écologie quantitative qui traite de l'analyse numérique des complexes de données. Contrairement à la biométrie, l'écologie numérique combine systématiquement les méthodes statistiques appropriées à l'écologie à des techniques numériques non statistiques (groupements, ordinations...), souvent sans référence à des distributions théoriques (Legendre et Legendre, 1998). Les méthodes mises au point dans ce cadre sont donc adaptées aux problématiques de l'écologie. Elles sont destinées à estimer la ressemblance entre les objets ou les variables, à grouper ces objets ou variables selon leur ressemblance, les ordonner dans un espace réduit pour faire ressortir leurs structures principales (gradients notamment), à modéliser les relations entre

des matrices de variables explicatives et descriptives, et à tester ces relations (Jongman et *al*., 1995).

En analyse multivariable, il existe deux grandes familles de méthodes: les méthodes de groupement et les méthodes d'ordination. Le groupement vise à séparer les objets en groupes mutuellement exclusifs, i.e. qu'aucun objet ne peut appartenir à deux groupes. L'ordination en espace réduit a pour but de représenter les données dans un nombre réduit d'axes (de dimensions) orthogonaux (indépendants) qui représentent les principales tendances ou structures de la variabilité des données (Legendre et Legendre 1998). On mentionnera ici quatre techniques de base: l'analyse en composantes principales (ACP), l'analyse factorielle des correspondances (AFC), l'analyse en coordonnées principales (ACoP) et le cadrage multidimensionnel non métrique (Legendre et Legendre, 1998).

3.2 Analyses canoniques

Les analyses canoniques sont des méthodes d'ordination en espace réduit. Alors que les méthodes citées précédemment visent à représenter la variation d'une matrice de données en un nombre réduit d'axes, les analyses canoniques visent, en revanche, à expliquer les relations entre deux matrices: une matrice de variables explicatives (ex: abondances d'espèces, données de maladies...) et une matrice de variables descriptives (ex: climat, physico-chimie du sol...). Les objets subissent donc deux ordinations successives: une combinaison linéaire des variables explicatives (matrice Y) par régression multiple, comme en ACP, puis les variables ajustées à ce premier modèle (nouvelle matrice $\hat{Y}$) subissent une seconde ordination par régression multiple sur les variables descriptives (matrice X). Les axes canoniques obtenus expliquent donc la variabilité des variables explicatives et sont également une combinaison linéaire des variables descriptives, combinaison qui explique le mieux possible cette variabilité. Parmi les ordinations canoniques, on utilise principalement l'analyse canonique des redondances (ACR) et l'analyse canonique des correspondances (ACC). L'ACR est la version canonique de l'ACP et conserve ainsi les distances euclidiennes entre les objets tandis que l'ACC est la version canonique de l'AFC et conserve les distances du Chi^2. On utilise l'ACC plutôt pour les matrices d'abondances d'espèces puisqu'elle ne tient pas compte des doubles 0 (double absence). Cependant, Legendre et Gallagher (2001) ont développé des transformations qui permettent d'utiliser les données d'abondances d'espèces en ACR (ou en ACP), et ainsi d'éliminer quelques problèmes liés à l'utilisation de l'ACC (ou de l'AFC) pour les abondances d'espèces. Legendre et Anderson (1999)

ont par ailleurs développé des tests par permutations qui utilisent l'ACR pour tester les plans d'analyse de variance (ANOVA) multifactorielle. Le plan d'ANOVA est codé et utilisé comme matrice de variables explicatives et l'ACR teste l'effet des facteurs et de leurs interactions à l'aide de tests par permutations. Cette approche novatrice a l'avantage de pouvoir tester des plans d'ANOVA avec des variables qui ne présentent pas une distribution normale ou qui approchent la normalité, essentielle à la validité de l'ANOVA, comme par exemple des données d'abondances d'espèces.

3.3 Applications à l'agronomie et à la protection des cultures

Bien que les analyses multivariables soient surtout utilisées en écologie numérique, depuis "l'impulsion" de Sokal et Sneath (1963) et sa contrepartie canadienne (Legendre et Legendre, 1979) on ne compte plus, en protection des cultures et en agronomie, les recherches fondamentales et appliquées qui ont recours aux analyses de données multivariables. La qualité et la fertilité des sols, en fonction de pratiques culturales et d'amendements divers, ont été mises en relation par analyses multivariables (Acosta-Martinez et *al*., 2004; Johansson et *al*., 1999; Petersen et *al*., 2003), dont les analyses canoniques (Jobin et *al*., 2003). La mise en oeuvre d'analyses multivariables, dont une proportion certaine d'analyses canoniques, en protection des cultures est surtout probante en malherbologie. Elles touchent des problématiques d'écologie appliquées aux agroécosystèmes (Kenkel et *al*., 2002), comme chez le maïs ou les céréales, les légumineuses ou le soja (Barberi et Mazzoncini, 2001; Bellinder et *al*., 2004; Dieleman et *al*., 2000 a et b). Ainsi, les études de Leeson et *al*. (1999 et 2000) en Saskatchewan et de Légère et Stevenson (2002) au Québec reflètent les effets des pesticides, des rotations et des antécédents culturaux sur les communautés de plantes nuisibles. Une même étude pourra intégrer malherbologie, entomologie et phytopathologie (de la Fuente et *al*., 2003; Dillard et *al*., 2004).

Au regard de la phytopathologie, les analyses multivariables sont éprouvées notamment en épidémiologie (Vernière et *al*., 2003), en résistance génétique variétale chez le soja (Burnham et *al*., 2002) et chez le pommier (Dewdney et *al*., 2003) ainsi qu'en étiologie à l'échelle spécifique (Lindqvist-Kreuze et *al*., 2003) et intra-spécifique (Barasubiye et *al*., 1995; Dusabenyagasani et *al*., 1999; Kaboré et *al*., 2001; Ménard et *al*., 2003). Pertinemment, l'analyse multivariable a concouru à la mise en évidence de sols réceptifs au *Fusarium* sp. chez le pois (Oyarzun et *al*., 1994) ou de sols suppressifs chez la pomme de terre au Québec (Martinez et *al*., 2002) ou, au

Canada, du potentiel d'amendements azotés à réprimer le flétrissement verticillien (Tenuta et Lazarovits, 2004).

Dans les études précitées, on a souvent eu recours à l'analyse canonique (Barberi et Mazzoncini, 2001; de la Fuente et *al*., 2003; Dieleman et *al*., 2000 a et b; Jobin et *al*., 2003). En phytopathologie, les analyses canoniques permettraient une meilleure exploitation des données que l'analyse univariable seule. En effet, l'ANOVA ne permet pas de comparer des infestations sur plusieurs années en raison de la forte variabilité d'une année à l'autre et de l'hétérogénéité des variables qui en découle généralement. Bailey et *al*. (2001) utilisent l'ACC pour caractériser le développement des principales maladies foliaires et radiculaires du blé sous plusieurs rotations combinées à plusieurs intensités de travail du sol pendant 9 ans. L'ACC a révélé des relations entre l'intensité de quelques agents pathogènes et les pratiques culturales (i.e., les agents pathogènes foliaires et le *Fusarium* associés au semis direct) alors que l'ANOVA ne les détectait pas. L'analyse canonique permettait également de mieux comprendre l'influence des principaux facteurs de l'écosystème sur le développement des maladies (Bailey et *al*., 2001). Parmi les ordinations canoniques, l'analyse canonique des redondances (ACR) est davantage utilisée, par exemple dans l'étude des communautés bactériennes ou de la faune du sol pour caractériser ou comparer les agroécosystèmes (Maire et *al*., 1999). L'ACR est traitée dans la synthèse de Kenkel et *al*. (2002) en malherbologie. Par son fort potentiel, l'analyse de redondance a montré la relation entre le statut socio-économique de paysans africains et les plantes mises en culture (Eilu et *al*., 2003); au Québec, l'ACR a contribué à expliquer les équilibres anion-cation en solution hydroponique chez la tomate de serre (Lopez et *al*., 2002). D'après Bailey et *al*. (2001), les analyses multivariables devraient être utilisées en association avec les analyses univariables, leur complémentarité permettant une compréhension plus complète des phénomènes étudiés.

CHAPITRE 1. Effet de la rotation et de l'amendement en compost urbain sur la sclérotiniose du soja dans deux sols

Sommaire: L'effet de la rotation du soja avec le maïs (2 ou 3 ans) et de l'amendement en compost urbain sur la sclérotiniose du soja (gravité de la maladie, nombre d'apothécies, survie des sclérotes du *Sclerotinia sclerotiorum*) a été comparé à celui de la monoculture de soja et de la fertilisation minérale sur deux sols (loam argileux et loam sableux) à Saint-Hyacinthe, dans le sud-ouest du Québec, entre 1999 et 2002. En 2002, la rotation 3 ans de maïs a montré un effet significatif sur la gravité de la maladie (DSI: disease severity index) dans le site argileux. La gravité a été fortement réduite par la rotation (5,2 %) par rapport à la monoculture (44,3 %). Dans le site sableux, l'interaction de la rotation 3 ans de maïs et de l'amendement en compost a présenté un effet significatif sur la gravité qui a été réduite à 37,8 % dans la rotation 3 ans de maïs amendée en compost comparé à 70,0 % en monoculture. L'analyse canonique des redondances (ACR) sur la matrice DSI-Apothécies en 2002 a confirmé l'effet suppressif de la rotation et révélé un effet favorable significatif du compost dans le site argileux. Le DSI était positivement corrélé à la monoculture et au compost, tandis que les apothécies étaient positivement corrélées au compost. Dans le site sableux, l'ACR sur la matrice DSI-Apothécies a confirmé l'effet suppressif de l'interaction. Seul le DSI était corrélé à la monoculture et à la fertilisation minérale, les apothécies n'étant corrélées à aucun traitement. L'utilisation d'analyses basées sur la régression multiple et les tests par permutations (Monte Carlo) pour tester le plan d'ANOVA (MANOVA) multifactorielle a procuré un test plus sévère de l'effet des traitements que l'ANOVA elle-même et a mené notamment au calcul de la fraction de variance expliquée par chacun des traitements de rotation et de fertilisation. Les traitements codés par des variables muettes ont pu être utilisés dans des ACR qui incluent des variables spatiales et environnementales pour construire des modèles minimaux qui expliquent la sclérotiniose, recherche qui sera présentée dans le chapitre 2. Grâce à la partition de la variance utilisée dans les analyses du chapitre 3, la fraction de variance expliquée par les traitements sera comparée aux autres composantes de l'écosystème incluses dans l'étude, à savoir la canopée, la physico-chimie et la microbiologie du sol, et les coordonnées spatiales.

Mots clés: *Sclerotinia sclerotiorum,* sclérotiniose du soja, rotation, compost urbain, régression multiple, analyse canonique des redondances, test par permutations.

Effect of crop rotation and urban compost amendment on *Sclerotinia* stem rot on soybean in two soils

Abstract: The effect of soybean rotations with corn (2/3-years) and urban compost amendment on *Sclerotinia* stem rot of soybean (disease severity, apothecia number, sclerotia survival), caused by *Sclerotinia sclerotiorum,* was compared with soybean monoculture and mineral fertilization on two soils (clay loam and sandy loam) at Saint-Hyacinthe, in southwestern Québec, from 1999 to 2002. In 2002, the 3-y-corn rotation had a significant effect on disease severity (DSI: disease severity index) at the clay loam site; DSI was greatly reduced by rotation (5.2%) compared to monoculture (44.3%). At the sandy loam site, the interaction of the 3-y-corn rotation with urban compost had a significant effect on DSI, which was reduced from 70.0% in the monoculture to 37.8% in the 3-y-corn rotation amended with compost. The canonical redundancy analysis (RDA) on the DSI-Apothecia matrix in 2002 confirmed the suppressiveness of the 3-y-corn rotation and revealed a significant conducive effect of compost at the clay loam site. The DSI and Apothecia were associated with compost. At the sandy loam site, RDA on the DSI-Apothecia matrix confirmed the suppressiveness of the interaction. The apothecia were not correlated with any (rotation or fertilization) treatment. The use of multiple regression-based analysis in multi-factorial (M)ANOVA design led to a more severe test of treatment effects than ANOVA and allowed to quantify the variation explained by each treatment.

Key words: *Sclerotinia sclerotiorum, Sclerotinia* stem rot of soybean, crop rotation, urban compost, multiple regression, canonical redundancy analysis, permutations test.

Introduction

Sclerotinia stem rot (SSR) of soybean (*Glycine max* L.) is caused by the soil-borne discomycete *Sclerotinia sclerotiorum* (Lib.) de Bary. *S. sclerotiorum* is a wide range pathogen attacking numerous cultivated and non-cultivated plant species, essentially dicotyledons, and has a worldwide distribution (Boland and Hall, 1994). The disease development in Northeastern America was associated with soybean culture intensification characterized by short or no rotation with non-host crops (Anderson, 1996), irrigation (Grau and Radke, 1984) or reduced row spacing (Workneh et *al*., 1996). The reduction of rotation tends to increase the soil-borne inoculum because sclerotia are able to survive more than five years in soil (Ben Yephet et *al*., 1993). Irrigation and reduced row spacing create more favourable temperature and humidity conditions for sclerotia carpogenic germination (apothecia) (Sun and Yang, 2000). In Ontario (Canada), the disease became a major soybean disease along with cyst nematode [*Heterodera glycines* (Ichinohe)], Phytophthora root rot [*Phytophthora sojae* (Kaufmann & Gerdemann)], and seedling diseases [*Pythium* spp., *Fusarium* spp., *Rhizoctonia solani* (Kühn), *Phomopsis* sp.] (Anderson and Tenuta, 2001). In Québec (Canada), SSR of soybean became a major threat for soybean production since 1996. Due to the particularly humid and cool weather, SSR caused 20% of yield losses on more than 2500 ha of soybean crop (Rioux, 1997).

In Australia, disease increasing incidence was attributed to substitution of traditional organic amendments by exclusive mineral fertilization (Asirifi et *al*., 1994). Organic amendments have been proven to be effective in controlling numerous soil-borne plant pathogens including *S. sclerotiorum* (Lazarovits, 2001), along with compost amendments (Kokalis-Burelle and Rodriguez-Kabana, 1994; Viana et *al.*, 2000). However, the ability of composts or organic amendments to control *Sclerotinia* diseases depends on local soil conditions and climate and therefore cannot be considered as universally efficient. Under particular conditions, compost amendments prove to increase the incidence of SSR on peas (Ferraz et *al*., 1999). While the impact of soil type and its interaction with the soil physico-chemical characteristics are poorly understood, it was reported that a higher sclerotia degradation was achieved in soil that had a higher clay content (Adams, 1975; Chambers and Hardie, 1964; Merriman, 1976). Carpogenic germination was also higher in fine textured loam than in sandy loam when sclerotia were placed at soil surface (Singh and Tripathi, 1996) or were shallowly buried (Harvey et *al*., 1994).

Management practices, including reduced or no-till, non-host crop rotations (Garcia-Garza et *al*., 2002), wide row spacing (Workneh et *al*., 1996), and reduced irrigation (Grau and Radke, 1984) are currently used to reduce the severity of SSR. Cultivars with early maturity, reduced height, resistance to lodging or cultivars with partial resistance (Cober et *al*., 2003; Nelson et *al*., 1991; Rousseau et *al*., 2004) can be integrated in management practices to reduce the incidence of the disease and therefore the amount of inoculum in infested fields. However, none of these integrated practices is able to efficiently control SSR. Moreover, their modes of action are poorly understood and do not permit to accurately predict their potential to control *Sclerotinia* disease.

This study aimed to determine whether crop rotation (with corn), an urban compost amendment and their interaction will influence SSR severity, carpogenic germination and sclerotia survival in two contrasted sites (clay loam and sandy loam).

Materials and Methods

Study sites

The study was conducted from 1999 to 2002 in two fields at the IRDA-CÉROM (Institut de Recherche et de Développement en Agroenvironnement ; Centre de recherche sur les grains inc.) research station, in Saint-Hyacinthe (Québec, Canada). The climate is cold temperate with averages of 208.6 frost-free days, a mean maximum daily temperature of 11.1ºC, and a mean minimum daily temperature of 1.3ºC (averaged during 1971 through 2000). Weather data were provided by the IRDA, Saint-Hyacinthe. These data were compared with the 30-year temperature and rainfall normals recorded at Environment Canada meteorological station in Saint-Hyacinthe (Environment Canada, 2004) (Appendix D). In one study site, soil was a clay to sandy-clay loam (Saint-Urbain series), and in the other, consisted of a loamy sand to sandy loam (Saint-Damase series).

Field history

At the clay loam site, there were three different crops in 1994, barley, soybean, and wheat; in 1995 there were barley, soybean, and sorghum; from 1996 to 1998 the whole site was covered by

alfalfa. Alfalfa was fertilized with 0-20-30 N-P-K. In 1996 and 1997 weeds were controlled by the herbicide Cobutox (2-4 DB, 2.0 Lha^{-1}) and with a rotary hoe in 1998. At the sandy loam site, corn was grown from 1994 to 1998. From 1994 to 1996 weeds were controlled with the herbicide Dual/Bladex 90 DF (cyanazine/metolachlore 2.5 Lha^{-1}/2.25 $kgha^{-1}$) and with a rotary hoe in 1997-1998. Conventional tillage was applied to both fields in all previous crops.

Experimental design

The experimental design was a split-plot with four blocks in which crop rotations consisted of the main plots and fertilizations the subplots. The rotation treatments were: 3-y-Corn = corn-corn-corn-soybean, 2-y-Corn = corn-corn-soybean-soybean, and a 4-y-soybean monoculture. The fertilization treatments were: NPK = mineral and UC = urban compost (Conporec inc., 2004). Main plots were 15 m x 24 m with 1 m between plots and were divided into two subplots (7.2 x 24 m) with 0.5 m of interplot space. Reduced tillage, applied to all plots, was one vibrocultor operation after spring fertilization, and one chisel plow operation after fall fertilization. All plots were mechanically weeded as needed by one vibrocultor operation followed by rotary hoe operations during weed germination and until the one-leaf stage of soybean (Fehr et *al*., 1971). Corn was weeded with the use of weeder operations until the seven leaf stage. Manual weeding was performed as needed to control excessive weed growth. Local herbicide (Glyphosate) application were used to control perennial weeds. Mineral fertilizer was manually applied in soybean plots, whose quantity varied according to the soil analysis and CPVQ recommendations (CPVQ, 1996). In corn, mineral fertilizer was applied with seeder in the row according to soil analysis and CPVQ recommendations. An additional liquid urea fertilizer (140 $kgN\ ha^{-1}$) was applied during the 6-7-leaf stage of corn. In 1999, 40 $t\ ha^{-1}$ of urban compost were applied in two applications of 20 $t\ ha^{-1}$ (spring and fall). Since a N deficiency was noticed in corn fertilized with compost (symptoms of leaves yellowing: White, 1999), the spring compost fertilization was reduced in all plots to 10 $t\ ha^{-1}$ in 2000-2002. Soybean plots were sown at a 18 cm row spacing, using an International 510 seeder, which would result in an expected population rate of 500 000 plants ha^{-1}. The soybean cultivar OAC Bayfield was chosen for its wide use in Québec and its susceptibility to SSR (Rioux, 1997). Corn plots were sown at a 76 cm row spacing, using a John Deere 7200 seeder, at an expected population rate of 80 000 plants ha^{-1}. The hybrid cultivar Pioneer 3893 was used. Air dried *S. sclerotiorum* sclerotia were manually applied on a 5.2 x 18 m surface in each plot at a rate of 20 to 40 sclerotia m^{-2}. Sclerotia originated from cleaning of soybean seeds harvested in 1998 in the Saint-Césaire area (Québec, Canada).

Data collection

Sclerotinia stem rot variables

Sclerotinia stem rot of soybean was assessed by disease severity, sclerotia survival and carpogenic germination from 2000 to 2002.

Disease severity

In 1999, plots were monitored for disease symptoms once a week starting on the 15th of August until soybean maturity. In 2000-2002, 50 plants per plot (25 north and 25 south of plots) were rated at the end of the growth season (stage R6-7; Fehr et *al*., 1971) according to a four-class disease severity scale where: 0, no symptom; 1, lesions on lateral branches; 2, lesions on main stem but little or no effect on pod-fill; 3, lesions on main stem, wilting, pods not or poorly developed, or dead plants. This scale was used to calculate the DSI as follows: $\sum$ (severity class * number of plants per class) * 100 / (total number of plants * total number of classes with symptoms) (Grau and Radke, 1984).

Apothecia counts

Carpogenic germination of sclerotia applied on the soil surface was assessed in 2000 to 2002 by counting the number of apothecia in two 0.75 m^2 quadrats per plot at a weekly frequency. Counts began when the soybean canopy was closed (end of June) and was stopped at soybean maturity. Apothecia counts were expressed as the number of apothecia m^{-2} $week^{-1}$.

Sclerotia survival

One hundred sclerotia were mixed in approximately 4 L of soil from the 0-10 cm soil layer in a mesh bag made with glass fiber insect screen that was closed with nylon bond. Two mesh bags per plot were buried (one north, one south) after sowing in spring 2000. The mesh bags were removed from the field just before fall chisel plow in order to assess sclerotia survival. The content of mesh bags was put in water for rapid soil desaggregation and was sieved at 2 mm under water flow to recover sclerotia. Sclerotia that had conserved their natural firmness were considered alive (van Toor et *al*., 2000). Surviving sclerotia were counted and placed in 100 mL of the soil from their original bag, and were conserved at 4°C in darkness until their return to the field in the next spring.

Analyses of soil and urban compost

Sampling

Samples for physical and chemical analyses were collected in the fields using a 5 cm diameter auger. Soil samples were analyzed in our laboratory or in a referred soil analysis laboratory for a range of standard physical and chemical properties. One sample consisted of three subsamples taken within a 0.5 m^2 plot, which were collected in three areas in 1999 and two areas in 2000-2002. Samples were collected in July along a north-south diagonal, were air dried and were sieved to 2.8 mm. Half of the 0-10 cm soil samples were not dried but were rather stored at 4°C and sieved at 6 mm just before taking mean weight diameter measurements. Urban compost analyses were performed by the CRIQ laboratory (Sainte-Foy, Canada) according to BNQ standards for compost quality (CAN/BNQ, 1996) (Table 1).

Physical analyses

The mean weight diameter (Kemper and Rosenau, 1986) was determined in order to evaluate the stability of aggregates. Forty g of 6 mm fresh sieved soil samples, collected and prepared as described above, were sieved in water by a sieving machine for 10 min. Two mm, 1 mm, 0.5 mm, and 0.25 mm sieves were used to separate wet aggregates. Twenty g of each sample were collected to determine sample water content. Aggregates of each size class were dried at 105°C, dispersed in a 5 gL^{-1} Hexametaphosphate solution for 10 min at 250 rpm and were wet sieved again to separate each size class. Primary particles were dried at 105°C and their weight was subtracted from the dry aggregates weight whose values were used to calculate the mean weight diameter: MWD = $\sum$ (mean diameter * aggregates weight) / sample dry weight. The field capacity (FC) was determined by weighting soil samples imbibed for 24 h, then drained by exerting material to a -10 kPa pressure, and dried at 105°C (Cassel and Nielsen, 1986). The organic matter (OM) content was determined by combustion: OM % = (weight at 105°C - weight at 420°C) / (weight of air dried soil) * 100 (CPVQ, 1988). The particle-size analysis, percentages of clay, silt and sand, were determined by the modified hygrometer method (Gee and Bauder, 1986).

Chemical analyses

The pH was measured with a glass-calomel electrode pH meter in distilled water and KCl buffer. The concentration of nutrients P, K, Mg, Ca, and Al in soil samples was determined by Mehlich III extraction method. C, N, and S concentrations were determined by LECO CNS 2000 ®.

Cation Exchange Capacity (CEC) was calculated from Mg, K and Ca concentrations (Mehlich III): CEC (meq/100) = [(7.5 - pH buffer) * 9] + [K] + [Ca] + [Mg] (AFEQ, 1990).

Statistical analyses

Normality of data was tested using PROC CAPABILITY procedure of the Statistical Analysis System (SAS for Windows V8, SAS Institute Inc., 2001), and homogeneity of variances was examined by plotting residuals versus predicted values using the PROC GLM and PROC PLOT procedures. Non-normal variables were transformed using appropriate transformations before performing Monte Carlo permutations tests (Legendre and Legendre, 1998). The split-plot option of CANOCO 4.5 (ter Braak and Smilauer, 2002) was used to perform univariate and multivariate permutations tests of rotation and fertilization effects on SSR parameters. The effects of rotation and fertilization treatments were tested separately in each site/soil. The site effect was tested by combining both experiments. As the soil type was not truly repeated, we only discussed the differences of rotation and fertilization effects between soils (Snedecor and Cochran, 1989).

The tests of CANOCO 4.5 split-plot option are based on canonical redundancy analysis (RDA: Jongman et *al*., 1995). This ordination method can be considered as a multivariate extension of multiple linear regression, i.e. it is a principal component analysis, modified to constrain the ordination axes to be linear combinations of a set of explanatory variables given in a separate matrix. Like multiple regression, RDA has a partial form that allows to control the effect of undesired variables, or variables whose effect is well known, which can be removed from the test. This property of RDA allows its use to test the correlations between the matrices of explanatory and descriptive variables, by the mean of Monte Carlo permutations tests. The design is coded by dummy variables as described by Legendre and Anderson (1999). These variables, coding for the rotation and fertilization treatments, are used as descriptive or covariable matrix in RDA (X and W matrix, respectively) while SSR variables are explanatory variables (Y matrix). Variables coding for the treatments whose effect wanted to be tested are in matrix X, and other variables coding for treatments are in matrix W (ter Braak and Smilauer, 2002). When the test is performed with CANOCO on one single explanatory variable, RDA becomes a multiple (partial) linear regression.

Results

Weather data

The three years where SSR variables were recorded (2000-2002) showed marked differences in the frequency and the amount of precipitation (Appendix D). During this period rainfall was under the normal based on measurements taken from 1971 to 2000 in Saint-Hyacinthe during May through September and during June through August (Environment Canada, 2004). This period spans the soybean flowering and grain filling period. During May through September rainfall, totals were of 457.7 mm in 2000, 299.7 mm in 2001 and 355.7 mm in 2002, compared to the 30-y normal of 478.3 mm. During the June through August period, total rainfall was of 264.7 mm in 2000, 222.3 mm in 2001 and 170 mm in 2002, compared to 299.3 for the 30-y normal (Appendix D).

Daily mean temperature for May through September was under the 30-y normal in 2000 and was globally warmer than normal in 2001 (except in July), and in 2002 (except in May and June) (Environment Canada, 2004). In 2000, mean daily temperatures were 0.1ºC, 1.1ºC, 1.3ºC, 0.3ºC and 0.5ºC under the 30-y normal during the months of May through August, respectively. In 2001, mean daily temperatures were 2.3ºC, 1.7ºC, 2.2ºC and 1.9ºC above 30-y normal in May, June, August and September, respectively. Mean daily temperature was 1.5ºC under 30-y normal in July. In 2002, mean daily temperatures were 1.8ºC and 0.9ºC under 30-y normal in May and June, while they were 0.6ºC, 1.5ºC and 3.3ºC above 30-y normal in July, August and September, respectively (Appendix D).

Analyses of soils and urban compost

The clay loam and the sandy loam sites were analysed separately. Table 1 shows the average values of selected physical and chemical properties of the urban compost (Conporec inc., 2004) and the two soils from the Saint-Hyacinthe IRDA-CÉROM research station in 1999 and 2002.

Effects of rotation and fertilization on individual SSR variables

In 2002, rotation and fertilization on clay loam site had a negative effect on DSI. Rotations significantly reduced DSI compared to soybean monoculture. DSI was 44.3% in monoculture while it was 22.6% in 2-y-corn, and 5.2% in 3-y-corn (P = 0.05). Urban compost fertilization

effect on disease severity with a DSI of 32.5% compared to 15.5% in mineral fertilization was not significant (P = 0.07) (Table 2). However, neither carpogenic germination nor sclerotia survival were significantly affected by rotation or fertilization. In 2001, there was a significant impact of fertilization on disease severity and sclerotia survival. The DSI was 4.0% in mineral fertilization compared to 7.7% in compost amended plots (P = 0.006). The sclerotia survival was of 13% in mineral fertilization and of 33% in urban compost amended plots (P = 0.001) (Table 2). Carpogenic germination was not significantly affected by rotation and fertilization treatments. In 2000, neither sclerotia survival nor carpogenic germination were significantly affected by rotation or fertilization.

At the sandy loam site in 2002, there was a significant interaction between rotation and fertilization on disease severity. DSI was reduced in 3-y-corn rotation amended with urban compost compared with all other treatment combinations. In this treatment combination, the DSI was of 37.8% compared with values ranging from 56.7 to 71.7% in the other treatment combinations (P = 0.02) (Table 2). As at the clay loam site, neither carpogenic germination nor sclerotia survival were significantly affected by rotation or fertilization. In 2001, compared to 2002, a significant inverse relationship between rotation and fertilization on disease severity was evident. The DSI was reduced in monoculture amended with a mineral fertilizer, which resulted in disease severity of 8.5% vs 11.4 to 15.1% in the other treatment combinations (P = 0.05) (Table 2). Neither carpogenic germination nor sclerotia survival were significantly affected by rotation or fertilization.

At the clay loam site in 2002, the difference between rotations and monoculture explained 36.4% of the variance in the DSI. In 2001, the effect of fertilization explained 39.6% of the variance in the DSI and for 31.6% of the variance in sclerotia survival (Table 3). Also in 2002, at the sandy loam site, the interaction between rotation and fertilization explained 14.8% of DSI variance. In 2001, this interaction explained 9.9% of DSI variance (Table 3).

Site effects on individual SSR variables

In 2002, disease severity was found to be significantly affected by the site (Table 4). While the DSI on clay loam was 24.0%, it was of 59.9% in sandy loam (P = 0.001). However, the site had no significant effect on carpogenic germination or sclerotia survival during year 2002 (Table 4). In 2001, the site had a significant effect on disease severity and carpogenic germination. The DSI

was of 5.9% at the clay loam site and of 11.8% at the sandy loam site (P = 0.001). Carpogenic germination was 0.21 apothecia m^{-2} at the clay loam site and 0.79 apothecia m^{-2} at the sandy loam site (P = 0.008). The site had no significant effect on sclerotia survival in 2001 (Table 4). In 2000, the site had a significant effect on carpogenic germination and sclerotia survival. Carpogenic germination was determined to be of 0.74 apothecia m^{-2} at the clay loam site and 2.27 apothecia m^{-2} at the sandy loam site (P = 0.001). Sclerotia survival was of 78% at the clay loam site and of 57% at the sandy loam site (P = 0.001) (Table 4). In 2002, the site explained 38.5% of the DSI variance. In 2001, it explained 38.2% of DSI variance and, 8.2% of the variance for carpogenic germination. In 2000, the site effect explained 24.8% of the carpogenic germination variance and, 17.7% of sclerotia survival variance (Table 4).

Effects of rotation and fertilization on SSR variable correlations

At the clay loam site in 2002, rotation and fertilization had a significant effect on the DSI-Apothecia correlation. The difference between the 3-y-corn rotation and other crop sequences explained 16% of the variance for the DSI-Apothecia correlation (P = 0.04), while the fertilization explained a 8.5% fraction of this correlation variance (P = 0.05) (Table 3). Moreover, this effect of fertilization tended to explain DSI-Survival and DSI-Apothecia-Survival correlations (P = 0.06, for both correlations). Fertilization effect explained 9.3 and 8.5% of the variance of these correlations, respectively (Table 3). The triplot with DSI-Apothecia-Survival correlations and treatments showed a first RDA axis (RDA I) correlated positively with urban compost and negatively with mineral fertilization, the second axis (RDA II) being correlated positively with monoculture and negatively with rotations (Fig. 1). The apothecia and sclerotia survival were correlated (Table 3); they were correlated positively with RDA I and negatively with RDA II. The DSI was slightly correlated with Apothecia but uncorrelated with Survival (Table 3), but was positively correlated with both RDA axes (Fig. 1). The correlation between Apothecia and Survival was not significantly affected by the treatments. In 2001, fertilization had a significant effect on all correlations (Table 3). The urban compost amendment explained 21.0% of the variance in the DSI-Apothecia correlation (P = 0.006), 32.2% of the variance for the DSI-Survival correlation (P = 0.006), 19.1% of the variance for the Apothecia-Survival correlation (P = 0.005), and 22.3 % of the variance for the DSI-Apothecia-Survival correlation (P = 0.006) (Table 3). The SSR variables were not correlated together and rotation did not significantly affect DSI-Apothecia, DSI-Survival or DSI-Apothecia-Survival correlations in 2001 (Table 3).

At the sandy loam site in 2002, the interaction of rotation with fertilization had a significant effect on DSI-Apothecia correlation (Table 3; Fig. 2). The interaction of treatments explained a 7.7% fraction of the correlation variance ($P = 0.05$) (Table 3). Both RDA I and RDA II axes were positively correlated with urban compost and corn rotations and were negatively correlated with mineral fertilization and monoculture (Fig. 2). The DSI and apothecia were not correlated (Table 3), but were each negatively correlated with RDA I. The DSI was correlated negatively with RDA II, and Apothecia positively (Fig. 2). DSI-Survival, Apothecia-Survival and DSI-Apothecia-Survival correlations were not significantly affected by the rotation and fertilization treatments. In 2001, rotation had a significant effect on Apothecia-Survival correlation. The difference between the 3-y-corn rotation and the other rotations explained 10.0% of this correlation variance ($P = 0.03$) but Apothecia and Survival were not correlated together (Table 3). Neither rotation nor fertilization had significant effects on DSI-Apothecia, DSI-Survival or DSI-Apothecia-Survival correlations in 2001.

Site effects on SSR variable correlations

In 2002, the site had a significant effect on DSI-Apothecia, DSI-Survival and DSI-Apothecia-Survival correlations. The difference between the clay loam site and the sandy loam site respectively explained 20.0, 19.2 and 13.3% of the variance of these three correlations ($P = 0.001$) (Table 4). In 2001, the site had a significant effect on DSI-Apothecia, DSI-Survival and DSI-Apothecia-Survival correlations. The site effect explained 22.2, 20.5 and 15.7% of the variance for these correlations. The site effect could also account for a marginal fraction of variance of 4.3% in the Apothecia-Survival correlation ($P = 0.07$) (Table 4). In 2000, the site had a significant effect on Apothecia-Survival correlation. Differences between sites explained 21.2% of the correlation variance ($P = 0.001$) (Table 4).

Discussion

Methodology

The multiple linear regression, and its partial form, were chosen for univariate analysis of the effects of treatments because they allowed the use of permutations tests in an ANOVA-like procedure. Indeed, the number of samples was low in each soil under study (n = 24), so it was

expected that the power of ANOVA would have been lower than the power of Monte Carlo permutations test and then, the more conservative test was adopted (Legendre pers. com.). In the multivariate analyses, the RDA and its partial form were then used in a MANOVA-like procedure again because of the low number of samples. Moreover, the use of multiple regression and RDA with variables coding for treatments to perform ANOVA(MANOVA)-like analysis provides exact F statistic and *P* probability, along with the fraction of explained variation explained by each treatment and interaction, equivalent to the classic ANOVA(MANOVA) analysis (Legendre and Anderson, 1999). According to Graham and Edwards (2001), the estimation of variance components is an important step in ecological analysis of variance, as variance components are the best estimate of the contribution of a given factor to variability in a response variable. Moreover, the decomposition of variance components provided by the multiple regression approach is equivalent to the more robust method recommended for ANOVA in ecological studies (Underwood, 1997).

Since permutations test do not need normality, these procedures could be used to test the effects of treatments on disease variables evaluated several years that generally do not reach normality (Bailey et *al*., 2001). This approach allows to include years or locations as additional factors, along with their interactions with treatments, and then to estimate their effects and relative contribution to the disease variables. Indeed, attention must be paid to the structure of the treatments in time, as their effects could be confounded. This is the case particularly with rotations, whose effect can only be fully achieved the last year of crop sequence. That is why the results of this study could only by analyzed year by year, from 2002 to 2000.

Effects of rotation and fertilization on individual SSR variables

At the clay loam site, the results of the effects of treatments on DSI were very contrasted and enclosed two phenomenons previously noticed: i) a lower incidence of SSR following corn or other non-host crop (Kurle et *al*., 2001); ii) the conducive effect of higher levels of OM added in the form of compost in bean plots (Ferraz et *al*., 1999). It was then concluded that the 3-y-corn rotation had a suppressive effect on disease severity while the urban compost was found conducive to SSR development (DSI x Apothecia correlation). This is the first time the conducive effect of compost was noticed for soybean. Furthermore, the disease severity exponentially decreased with increasing proportion of corn in the rotation, despite the conducive effect of compost amendment. Disease severity in 3-y-corn was very low (5.2%) compared to other crop

sequences and, even if no economic threshold for soybean incidence was defined in Québec, this result allows to recommend the rotation with corn for at least three years as an efficient management practice for the control of SSR on soybean. In this experiment, the cultivar OAC Bayfield was chosen for its susceptibility to SSR (Rioux, 1997). Consequently the integration of more resistant cultivars with rotation could provide an efficient strategy to reduce or suppress the disease. Kurle et *al*. (2001) noticed that planting the most resistant cultivar was the practice that reduced the most SSR incidence compared to non-host crop rotation or no-till.

The mean apothecia number estimated was very low compared to previous studies held in Northeastern America on silt loam (Kurle et *al*., 2001; Mueller et al., 2002) or fine textured organic soil (Garcia-Graza et *al*., 2002). No studies reported results of *S. sclerotiorum* carpogenic germination on clay loam. The lowest apothecia number was measured in 2002, the year with lower total rainfall for the June to August period. As apothecia are very susceptible to the variation of soil, air humidity, light intensity and temperature (Sun and Yang, 2000), the effects of treatments were tested on each weekly count as suggested by Kurle et *al*. (2001), but no significant effects were found either.

As noticed in this study, no difference in sclerotia survival following rotation with non-host crops was reported in previous studies (Maheu, 1999; Mueller et *al*., 2002). However, little information is available about the effects of rotation on sclerotia survival, particularly for SSR of soybean, but such results were also reported for bean crop (Schwartz and Steadman, 1978) or canola (Williams and Stelfox, 1980).

This was the first time an enhancement of sclerotia survival by compost was noticed (2001; Table 2). Ferraz et *al*. (1999) already reported higher disease incidence and carpogenic germination following compost amendment but sclerotia survival was not evaluated. In contradiction with this result, most of the references about the effects of organic amendments on sclerotia survival reported significant suppressiveness of urban compost (Appendices A and C), or fresh organic amendments (Nico et *al*., 2003), in controlled conditions. The soils studied by Nico et *al*. (2003) were silty loams. Such suppressive effect was also reported in fields affected by *Sclerotinia* soft rot of lettuce (caused by *S. sclerotiorum*) but in loamy sand (Asirifi et *al*., 1994).

The use of multiple regression allowed to determine the fraction of variation explained by the treatments. At the clay loam site, the fractions of Survival and DSI explained variation (in 2001 and 2002, Table 3) were high compared with the unexplained fraction, which is composed of pure spatial and environmental variation (including soil, canopy and climatic variation), more a stochastic fraction of variation. These results suggest that the effect of treatments constitutes one of the major factor of DSI or Survival variation at the clay loam site. The relative importance of treatments compared to spatial and environmental factors will be discussed in Chapter 3.

At the sandy loam site, the effect of the rotation and fertilization interaction in 2002 was opposite to the 2001 effect (Table 2). As the soil was particularly crusted in mineral fertilization plots (especially in clay loam), the soybean emergence was very low compared to compost amended plots, so we had to re-sow the mineral-amended plots in 2001. As the resown soybean entered flowering stage (R1) about one week later than the soybean in compost plots, it could have partly escaped the disease. No similar effect was detected in clay loam, but the disease incidence was much lower. Moreover, in 2001, the 2-y-corn rotation plots changed corn for soybean which led to higher variability in the plots micro-environment. These two facts may explain, in part, the unexpected result of the treatments interaction in 2001. Nevertheless, this interaction effect confirmed the suppressive potential of rotation on disease severity noticed in clay loam and in previous studies (Garcia-Garza et *al*., 2002; Kurle et *al*., 2001). Furthermore, these results support the view that no single practice will lead to suppression of this soil-borne disease in most soils (Bailey and Lazarovits, 2003; Hornby, 1983).

At the sandy loam site, the number of apothecia was much lower than previously noticed in silt loams (Kurle et *al*., 2001; Mueller et *al*., 2002). The number of apothecia reported at the sandy loam site from 2000 to 2002 were slighly lower, but similar with those reported by Garcia-Garza et *al*. (2002) during a 4 years experiment in a sandy loam in Ontario.

According to the multiple regression analyses, the fraction of variation explained by the treatments was much lower at the sandy loam site, compared with the clay loam site (Table 4). This suggested that the effects of treatments occurred in interaction with the soil type and emphasized the need for further research on the mechanisms that could explain disease suppression with particular attention to their interactions with the soil physical characteristics.

Site effects on individual SSR variables

As the effect of treatments was different between site/soil for DSI and sclerotia survival, it was hypothesized that the sandy loam was highly conducive to the disease compared with clay loam because of the highest rate of carpogenic germination. However, apothecia explained a very small amount of DSI variation in both soils, as shown by multiple regression between the *Sclerotinia* variables (Table 3). Other factors, yet undetermined, should be involved in conduciveness of sandy loam to SSR. Thus, in sandy loam the effects of treatments remained weaker and only the joint effect of rotation and urban compost could significantly reduced the disease severity.

Effects of rotation and fertilization on SSR variable correlations

At the clay loam site, the RDA analysis on DSI-Apothecia association confirms the conducive effect of compost, that became significant in 2002, when introducing Apothecia in the analysis (Table 3). Thus, a suppressive effect of compost was rejected for the DSI-Apothecia matrix in clay loam, while the suppressive effect of rotation was confirmed. The disease severity was higher in compost-amended plots probably because of its stimulating effect on carpogenic germination. This effect may be linked to the capacity of compost to reduce the crust that formed a barrier to stipes-forming-apothecia emergence as it did for soybean plantlets emergence (particularly in 2001). The inhibiting effect of a physical barrier was verified with mulch (Ferraz et *al*., 1999) and supported by the fact that only the sclerotia from the first 5 cm of soil are able to produce apothecia (Schwartz et Steadman, 1978). The effect of compost could also be related to the water content of soil, as the sclerotia need high soil moisture to germinate (Hall, 1994). However, apothecia are correlated positively with RDA I, which was correlated positively with compost and monoculture, and to a lesser extend, to 2-y-corn (Fig. 1). Thus, in 2002 Apothecia seems to be associated with the crop sequences with the highest soybean cover, along with compost amendment. This trend was consistent with the fact that apothecia generally not develop until the crop cover is closed (Morrall and Dueck, 1982), indeed the corn cover remained less dense than soybean cover.

The analysis on DSI-Survival association showed that both variables tended to rise in compost-amended plots in 2002, but were not correlated (Table 3), though the Survival and Apothecia were highly correlated together and the compost tended to affect the DSI-Apothecia-Survival association (Table 3). The occurrence of a suppressive effect of both rotation and compost was rejected for these correlations. The effect of compost probably affected Apothecia through its

effect on sclerotia survival, then apothecia development rose the potential of disease severity. Indeed, apothecia are highly susceptible to the microclimate conditions under canopy, and the ascospores they produce are able to survive on soybean about two weeks (Phillips, 1993) if the moisture conditions are not favorable for germination. This might explain why DSI and Apothecia or DSI and Survival were not correlated, but DSI and Survival were both associated to the effect of compost (Fig. 1).

At the clay loam site, the effect of compost dominated in 2001, probably because the effect of rotation was not fully testable as not all plots had returned to soybean. Again, the occurrence of a suppressive effect of compost was rejected from 2001. The SSR variables were not correlated in 2001 (Table 3). On DSI-Survival, compost effect was similar with 2002, which confirmed this trend of compost effect in clay loam (Table 3). In 2002, DSI and Survival were not correlated, but higher sclerotia survival in compost probably enhanced DSI indirectly through the production of apothecia. However, the strong effect of compost on DSI-Apothecia correlation in 2001 was probably dominated by the effect on DSI, from which compost explained 39.6% of variation (Table 3). The impossibility to link significantly Apothecia to DSI could be explained by the survival of ascospores released by apothecia, as previously discussed (Ferraz et *al*., 1999; Phillips, 1993) or by the survival of apothecia themselves and stipes-forming-apothecia. Indeed, apothecia and stipes were reported to dry and be rehydrated without dying (Boland and Hall, 1987). The effect of rotation on Apothecia-Survival at the clay loam site was significant in 2000, but this effect was due to the effect of 2-y-corn that showed reduced survival compared to monoculture.

At the sandy loam site, the significant effect of the interaction Rotation x Fertilization on DSI-Apothecia in 2002 was mainly due to the effect of the interaction on DSI, that showed a strong association of DSI with monoculture and mineral fertilization (Tables 2-3). Apothecia were correlated negatively with RDA I, which was negatively correlated with NPK and monoculture, and was positively correlated with RDA II, which was positively correlated with 2-y-corn (Fig. 2). However, a suppressive effect of rotation and urban compost was confirmed for the DSI-Apothecia matrix at the sandy loam site. Apothecia were not correlated with DSI (Table 3), and seemed to be associated with the soybean-dominated crop sequences and mineral fertilization. This trend was inconsistent with previous studies that concerned crop rotation and SSR. Indeed, Maheu (1999) found no significant difference in carpogenic germination under corn, wheat or

soybean in a silty loam at Saint-Hyacinthe research station. Conversely, Garcia-Garza et *al*. (2002) found a lower mean number of apothecia in a fine textured organic soil, under corn or wheat, compared with soybean. The strong dependence of carpogenic germination on soil texture (Teo et Morrall, 1985a), climatic conditions and their interactions (Sun and Yang, 2000) could explain these apparently contradictory results. The rotation and fertilization treatments had no significant effects on the other correlations in 2002, that confirmed their lower influence on SSR in sandy loam compared to clay loam.

Site effect on SSR variable correlations

As disease severity was the most affected variable regarding site (Table 4), this also explained why associations that included DSI were the most affected. However, carpogenic germination was greater at the sandy loam site in 2001 and 2000, while sclerotia survival was lower in 2000. This confirmed the importance of apothecia as the active inoculum, even if carpogenic germination was poorly correlated with disease severity among years. It was hypothesized that the sandy loam was more conducive to carpogenic germination because the crust was thin or absent compared to clay loam. Although the presence of sand made the soil dry more rapidly, the moisture in sandy loam probably remained sufficient for carpogenic germination, at least in 2001 and 2000 where precipitation remained consistent from June to August compared with 2002. Garcia-Garza et *al*. (2002) reported an opposite situation in Ontario with two similar soil types, a sandy loam and a fine textured organic soil. On four years, the mean number of apothecia was much higher in the fine textured soil than in sandy loam. The presence of OM in the fine textured soil was probably responsible for the difference with the present results as the clay loam studied here was poor in OM. More investigations are obviously needed to confirm this assumption which supports the conducive effect of urban compost observed in clay loam in the present study.

It is increasingly accepted that the modern agricultural systems are not able to provide sustainable food and fiber production along with viable ecosystem fonctions (Matson et *al*., 1997). Recently, the introduction of ecological theories to explain and propose strategies of ecosystem development (Odum, 1969) in agriculture and soil science (Anderson and Domsch, 1990) allowed the emergence of an ecosystemic approach of agronomy. This re-direction was largely stimulated by the harmful consequences of exclusive mineral fertilization and massive pesticide use on the soil erosion and water pollution. Thus, soil conservation techniques as reduced or no-

till, residue management and organic fertilization were recovered from the past and stimulated the development of actualized techniques to reclaim ecosystem fonctions, soil fertility or disease control, particularly soil-borne diseases (Bailey and Lazarovits, 2003). The results presented here sustained the potential of such an approach for the control of SSR of soybean. The rotation with non-host crop was efficient to reduce the disease incidence, alone or in combination with urban compost. The addition of OM by compost amendment proved its potential to reduce the disease incidence in sandy loam, but appeared disease conducive at the clay loam site. This highlighted the complexity of the soil system and OM dynamic (Bailey and Lazarovits, 2003) and confirmed the hypothesis stating that the rotation and fertilization treatments interact with soil and OM properties to influence SSR on soybean development.

The introduction of multiple regression-based techniques issued from numerical ecology, to test the effects of treatments and separate the variance components of the disease variables, has proved its efficacy to explain the effects of rotation, fertilization and their interaction. By their wide range of applications and the clarity of the representations, these techniques are very promising to stimulate the development of the ecosystemic approach of agricultural and phytopathological problems, along with the ecological use and interpretation of multi-factorial ANOVA, or MANOVA, designs which are very efficient tools for soil ecologists and agriculture researchers (Graham and Edwards, 2001). In the next two chapters, multiple regression, redundancy analyses and their partial forms are used to build minimal models including the most parsimonious sets of variables that explain SSR variables (Chapter 2) or to partition their variance by canopy, soil physico-chemistry, soil microbiology, spatial coordinates, as well as rotation and fertilization treatments matrices (Chapter 3).

Acknowledgements

The author acknowledges the Conseil des recherches en pêche et en agroalimentaire du Québec (CORPAQ) and the Fédération des producteurs de cultures commerciales du Québec (FPCCQ) financial support for this study. The author gratefully acknowledges Drs. D. Borcard and P. Legendre for their precious help and skillful assistance in the statistical analyses improvement. The author is also grateful to Roselyne Labbé for reviewing this chapter.

Table 1: Average values of selected physical and chemical properties of an urban compost and two soils from Saint-Hyacinthe IRDA-CÉROM research station in 1999 and 2002.

Property	Clay Loam		Sandy Loam		Urban Compost[z]
	1999	2002	1999	2002	
Clay (%)	34.9		10.0		-
Silt (%)	21.7		15.0		-
Sand (%)	43.5		74.1		-
MWD[y]	1.89	0.56	0.21	0.11	-
OM (%)[x]	2.8	3.0	2.7	3.1	72.0
FC (%)[w]	32.3	34.8	24.3	27.7	131.6
pH	6.72	6.63	7.01	7.11	7.48
CEC (meqL-1)[v]	17.9	17.6	12.7	13.8	99.5
C (total, %)[u]	1.3	1.3	1.3	1.8	35.1
N (total, %)	0.13	0.09	0.14	0.09	1.21
C/N	9.8	15.1	9.8	20.6	29.0
S (total, %)	0.023	0.042	0.014	0.034	ND[s]
P (ppm)[t]	63	55	225	230	2218
K (ppm)	241	218	201	220	6498
Ca (ppm)	2099	2034	1779	2113	28911
Mg (ppm)	337	293	88	92	2609
Al (ppm)	912	828	817	995	ND

[z] Mean of four samples analysed by CRIQ laboratory (Sainte-Foy QC, Canada) according to BNQ standards for compost quality (CAN/BNQ 1996)

[y] Mean Weight Diameter = ∑ (mean diameter * aggregates weight) / sample dry weight (Kemper and Rosenau 1986)

[x] Organic Matter (%) = (weight at 105°C-weight at 420°C) / (weight of air dried soil) * 100 (CPVQ, 1988)

[w] Field Capacity (Cassel and Nielsen 1986)

[v] Cation Exchange Capacity was calculated: CEC(meq/100) = [(7.5 - pH buffer) * 9] + [K] + [Ca] + [Mg] (AFEQ, 1990)

[u] C, N, S concentrations determined by LECO CNS 2000 ®

[t] P, K, Ca, Mg, Al determined by Mehlich III extraction method

[s] ND: non determined.

Table 2: Mineral fertilization, urban compost and rotation effects on SSR variables DSI, *Sclerotinia sclerotiorum* sclerotia survival and carpogenic germination in clay loam and sandy loam sites in Saint-Hyacinthe, from 2000 to 2002.

		Clay loam			Sandy loam		
		Mineral	Compost	Rotation	Mineral	Compost	Rotation
Year	Rotation[z]			mean			mean
			DSI (%)				
2000	S/S	0.8	6.3	3.6	3.7	5.3	4.5
2001	C/C/S	4.7	7.2	5.9	15.1a[y]	12.3a	13.7
	S/S/S	3.4	8.2	5.8	8.5b	11.4a	10.0
	Fertilization mean	4.0a[x]	7.7b		11.8	11.9	
2002	C/C/C/S	4.0	6.3	5.2a	67.0a	37.8b	52.4
	C/C/S/S	10.3	34.8	22.6b	56.8a	56.7a	56.2
	S/S/S/S	32.3	56.3	44.3b	70.3a	71.7a	70.0
	Fertilization mean	15.5	32.5		64.7	55.0	
			Carpogenic germination (# apothecia m^{-2})				
2000	C/C	0.93	0.89	0.91	1.28	3.64	2.46
	S/S	0.71	0.61	0.66	1.36	2.53	1.95
	Fertilization mean	0.83	0.65		1.65	2.89	
2001	C/C/C	0.42	0.17	0.29	1.17	2.08	1.62
	C/C/S	0.17	0.08	0.12	0.17	0.33	0.25
	S/S/S	0.25	0.17	0.21	0.33	0.67	0.50
	Fertilization mean	0.28	0.14		0.55	1.03	
2002	C/C/C/S	0.03	0.05	0.04	0.18	0.09	0.13
	C/C/S/S	0.14	0.27	0.20	0.21	0.21	0.21
	S/S/S/S	0.03	0.27	0.15	0.25	0.21	0.23
	Fertilization mean	0.07	0.20		0.21	0.17	
			Sclerotia survival (%)				
2000	C/C	76	82	79	48	64	56
	S/S	84	83	83	61	61	61
	Fertilization mean	78	78		55	59	
2001	C/C/C	15	41	25	29	12	19
	C/C/S	8	28	15	28	17	21
	S/S/S	18	30	23	36	28	32
	Fertilization mean	13a	33b		31	18	
2002	C/C/C/S	11	16	14	14	6	10
	C/C/S/S	8	19	13	13	11	12
	S/S/S/S	12	17	14	23	16	19
	Fertilization mean	10	17		17	11	

[z] C = corn, S = soybean.

[y] In sandy loam, and for each year, values followed by the same letter are not significantly different ($P \leq 0.05$) according to ANOVA-like analysis performed with split-plot option of CANOCO 4.5.

[x] In clay loam, and for each year mean values followed by the same letter are not significantly different ($P \leq 0.05$) according to ANOVA-like analysis performed with split-plot option of CANOCO 4.5.

Table 3: Linear regressions and effects of rotation and fertilization in (M)ANOVA-like analysis on SSR variables in clay loam and sandy loam sites in Saint-Hyacinthe, in 2001 and 2002.

SSR variables (correlations)[z]	*Source of variation*		Clay loam			Sandy loam		
		df	Trace	F	P[y]	Trace	F	P
				2002				
DSI	***Rotation***	2	36.4	11.4	0.05*	19.8	5.4	0.21
	Fertilization	1	10.2	4.2	0.07	7.2	3.7	0.08
	Rot x Fert	2	3.8	1.6	0.51	14.8	8.3	0.02*
Survival	***Rotation***	2	0.1	0.02	0.96	7.0	1.7	0.06
	Fertilization	1	8.5	2.9	0.14	6.9	1.2	0.31
	Rot x Fert	2	1.2	0.2	0.83	1.3	0.1	0.88
DSI x Apothecia		1	13.5	3.4	0.06	0.02	0.8	0.36
(r_{DA} = 0.37/0.21)	***Rotation***	2	16.0	4.3	0.04*	11.6	1.7	0.44
	Fertilization	1	8.5	3.0	0.05*	4.0	1.9	0.18
	Rot x Fert	2	3.5	0.5	0.78	7.7	1.7	0.05*
DSI x Survival		1	0.0	0.0	1	23.6	6.8	0.01*
(r_{DS} = 0.26/0.48*)	***Rotation***	2	18.3	2.6	0.13	17.2	2.3	0.14
	Fertilization	1	9.3	3.5	0.06	7.1	1.9	0.18
	Rot x Fert	2	2.5	0.4	0.84	8.0	1.1	0.40
DSI x (Apothecia x Survival)		2	13.5	1.6	0.06	26.4	3.8	0.04*
(r_{AS} = 0.71/-0.08)**	***Rotation***	2	14.8	2.0	0.17	12.6	1.7	0.22
	Fertilization	1	8.5	3.0	0.05*	5.0	1.5	0.23
	Rot x Fert	2	2.8	0.5	0.85	5.6	0.9	0.53
				2001				
DSI	***Rotation***	2	0.0	0.0	1	17.4	3.2	0.37
	Fertilization	1	39.6	17.6	0.006**	0.0	0.0	0.94
	Rot x Fert	2	4.0	1.8	0.23	9.9	5.4	0.05*
Survival	***Rotation***	2	6.3	2.3	0.19	4.0	1.3	0.51
	Fertilization	1	31.6	4.2	0.001**	6.3	1.7	0.25
	Rot x Fert	2	3.1	4.2	0.17	1.2	0.3	0.88
DSI x Apothecia		1	1.0	1.4	0.26	1.0	0.04	0.84
(r_{DA} = 0.03/-0.07)	***Rotation***	2	1.3	0.1	1	11.7	1.9	0.64
	Fertilization	1	21.0	4.1	0.006**	3.0	0.7	0.51
	Rot x Fert	2	2.0	0.4	0.66	5.3	1.3	0.30
DSI x Survival		1	9.0	1.4	0.26	0.0	0.05	0.82
(r_{DS} = -0.3/-0.06)	***Rotation***	2	2.6	0.4	0.64	10.4	2.1	0.37
	Fertilization	1	32.2	18.9	0.006**	1.8	0.5	0.66
	Rot x Fert	2	4.0	2.3	0.14	5.1	1.6	0.25
Apothecia x Survival		1	0.5	0.1	0.76	7.2	1.7	0.15
(r_{AS} = 0.18/-0.27)	***Rotation***	2	6.4	0.9	0.43	10.0	3.1	0.03*
	Fertilization	1	19.1	6.6	0.005**	4.7	1.2	0.36
	Rot x Fert	2	2.6	0.5	0.72	1.3	0.2	0.96
DSI x (Apothecia x Survival)		2	9.7	0.7	0.50	0.6	0.04	0.95
	Rotation	2	2.6	0.4	0.89	8.9	1.6	0.64
	Fertilization	1	22.3	5.9	0.006**	3.2	0.7	0.60
	Rot x Fert	2	2.6	0.7	0.53	3.6	0.8	0.49

[z] Linear correlation coefficients are given for each pair of SSR variables (in clay loam/sandy loam): DSI-Apothecia (r_{DA}), DSI-Survival (r_{DS}) and Apothecia-Survival (r_{AS}); [y] probabilities are given according to Monte Carlo permutation test (999 permutations): *, ** significant at $P \leq 0.05$ and $P \leq 0.01$.

Table 4: Site effects in combined (M)ANOVA-like analysis on SSR variables in clay loam and sandy loam sites in Saint-Hyacinthe, from 2000 to 2002.

	Site effect			
Y variables	**df**	**Trace**	**F**	**P**
2002				
DSI	1	38.5	27.1	0.001**
Apothecia	1	1.6	0.7	0.45
Survival	1	0.0	0.0	0.99
DSI x Apothecia	1	20.0	11.3	0.001**
DSI x Survival	1	19.2	11.5	0.001**
DSI x Apothecia x Survival	1	13.3	7.3	0.001**
2001				
DSI	1	38.2	18	0.001**
Apothecia	1	8.2	4.0	0.008**
Survival	1	0.4	0.2	0.64
DSI x Apothecia	1	22.2	8.2	0.002**
DSI x Survival	1	20.5	8.6	0.002**
Apothecia x Survival	1	4.3	2.2	0.07
DSI x Apothecia x Survival	1	15.7	5.8	0.003**
2000				
Apothecia	1	24.8	16.3	0.001**
Survival	1	17.7	10.7	0.001**
Apothecia x Survival	1	21.2	13.4	0.001**

[z] Probabilities are given according to Monte Carlo permutation test (999 permutations): *, ** significant at $P \leq 0.05$ and $P \leq 0.01$.

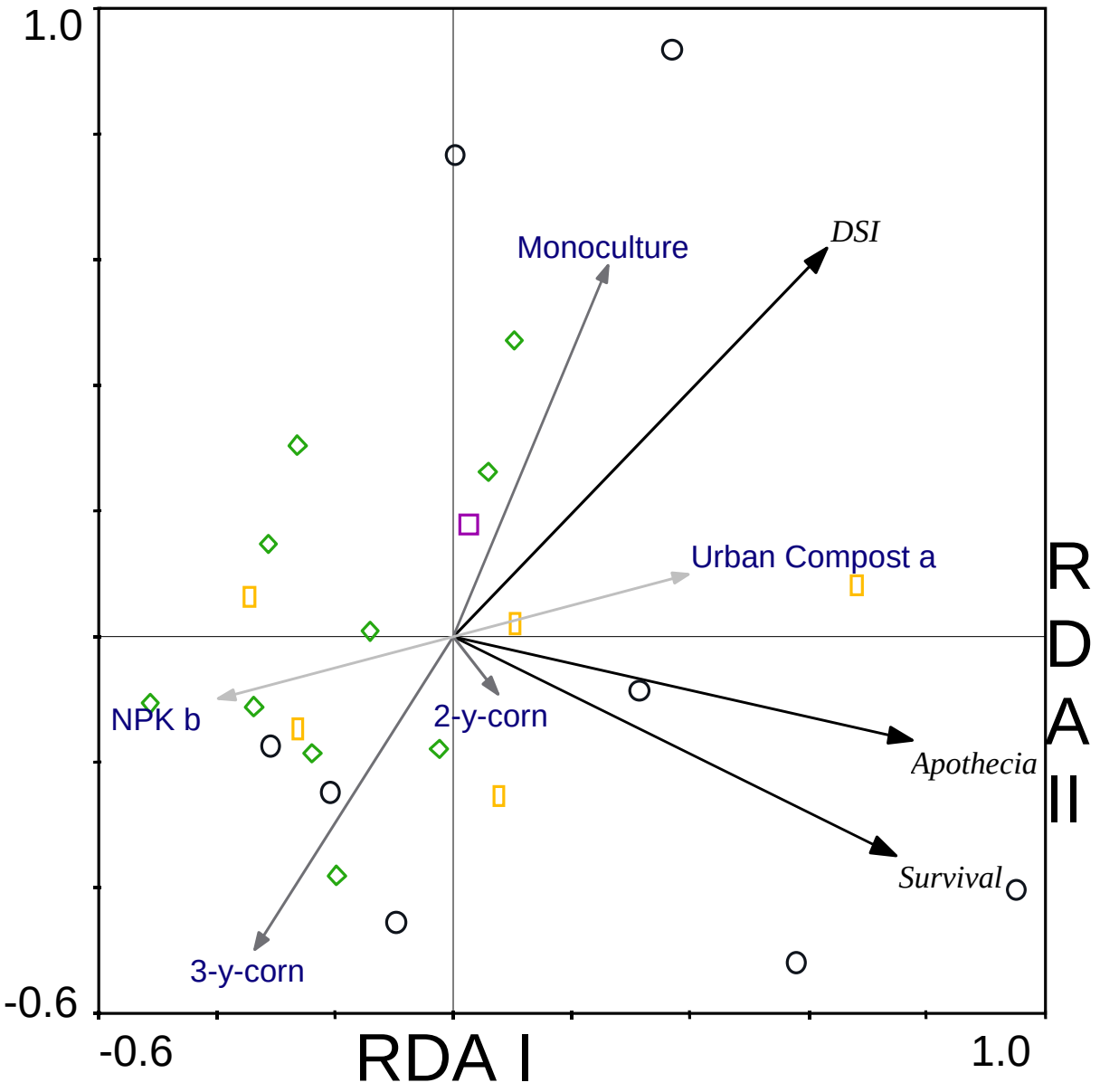

Figure 1. Clay loam site, 2002: canonical redundancy analysis (RDA) triplot of rotation, fertilization and *Sclerotinia* stem rot (SSR) variables [disease severity (*DSI*), carpogenic germination (*Apothecia*) and sclerotia survival (*Survival*)]. For fertilization, different letters indicate significant differences ($P \leq 0.05$) following MANOVA-like analysis performed with split-plot option of CANOCO 4.5. Triplots are represented following type II scaling (correlation triplot). Grey arrows indicate rotation and fertilization treatments, and black bold arrows SSR variable vectors. Samples are classified by soil type with □ clay, ◊ clay loam, ○ sand-clay loam, ▯ sand-clay.

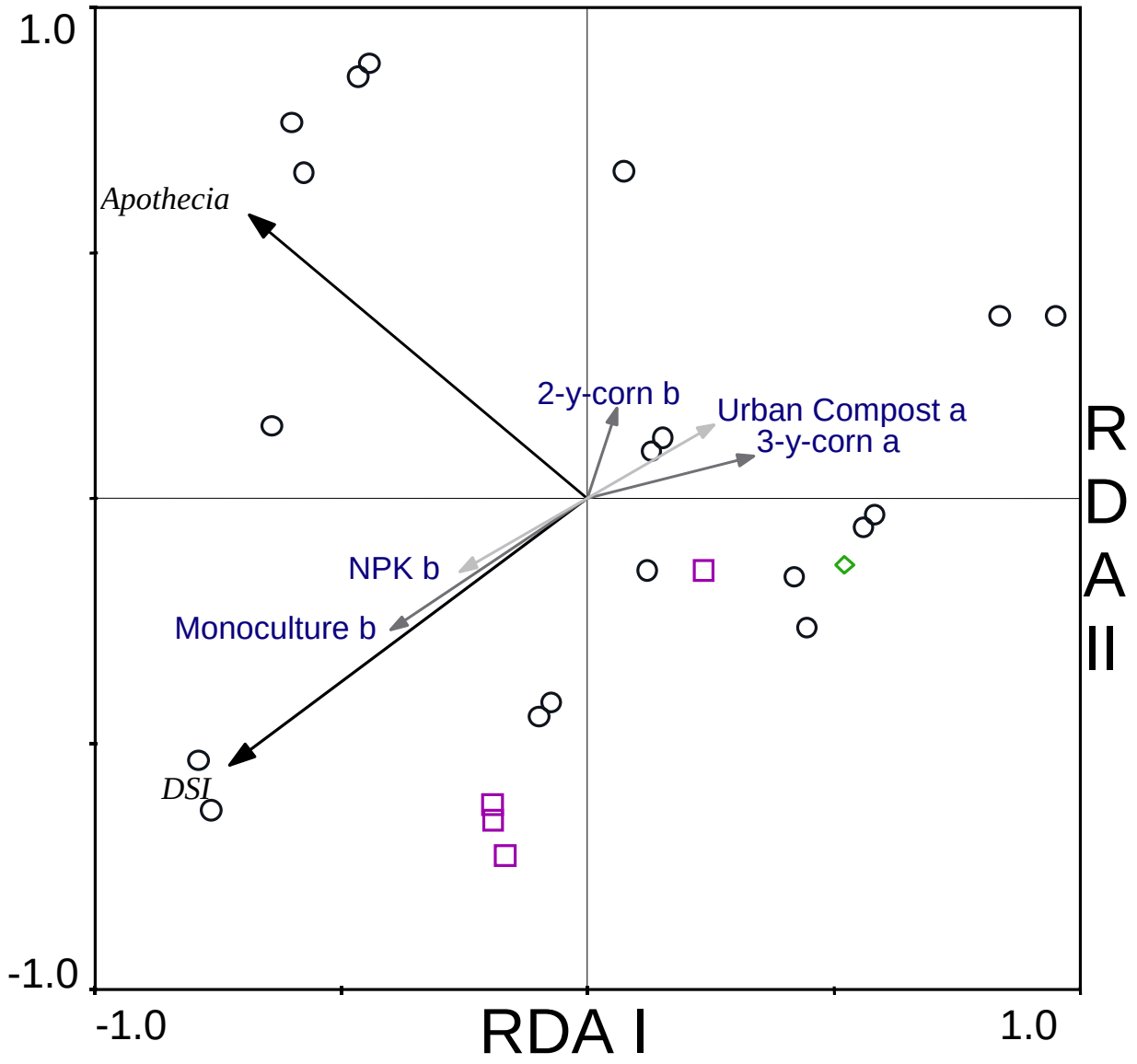

Figure 2. Sandy loam site, 2002: canonical redundancy analysis (RDA) triplot of the interaction rotation x fertilization and *Sclerotinia* stem rot (SSR) variables [disease severity (*DSI*), carpogenic germination (*Apothecia*)]. For the interaction, different letters indicate significant differences ($P \leq 0.05$) following MANOVA-like analysis performed with split-plot option of CANOCO 4.5. Triplots are represented following type II scaling (correlation triplot). Grey arrows indicate rotation and fertilization treatments, and black bold arrows SSR variable vectors. Samples are classified by soil type with □ clay, ◊ clay loam, ○ sand-clay loam.

CHAPITRE 2. Effets multivariables du couvert végétal, de la physico-chimie et de la microbiologie du sol sur la sclérotiniose du soja en relation avec la rotation et l'amendement en compost urbain

Sommaire : Dans le chapitre 1 précédent, l'analyse canonique des redondances (ACR) a confirmé l'effet suppressif de la rotation avec le maïs sur la gravité de la sclérotiniose (*Sclerotinia sclerotiorum*) chez le soja et révélé un effet favorable significatif du compost sur la gravité de la sclérotiniose dans le site argileux. La régression multiple et les tests par permutations (Monte Carlo) pour tester le plan d'ANOVA (MANOVA) multifactorielle ont mené notamment au calcul de la fraction de variance expliquée par chacun des traitements de rotation et de fertilisation. Dans le présent chapitre 2, les effets de plusieurs variables de couvert végétal, de physico-chimie et de microbiologie du sol sur la sclérotiniose ont été étudiés dans les loam argileux et loam sableux à l'aide de la régression multiple et de l'analyse canonique des redondances (ACR). La forme partielle de ces analyses a permis de contrôler l'effet des pratiques culturales (rotation 2-3 ans de maïs / monoculture de soja et fertilisation minérale / compost urbain), ou des variables spatiales sur les variables de sclérotiniose. Des modèles minimaux ont regroupé les variables qui expliquent le mieux la variation de la survie des sclérotes du *S. sclerotiorum*, de leur germination carpogénique, de la gravité de la maladie et de leurs corrélations. Au site argileux, la rotation 3 ans de maïs a réduit la gravité de la maladie par la réduction de la biomasse des adventices dont le couvert favorisait la germination carpogénique. Le compost urbain a favorisé la gravité de la maladie et la survie des sclérotes dans ce sol, effets expliqués par un meilleur drainage du sol en surface. En revanche, l'azote est corrélé positivement à l'effet suppressif de la survie des sclérotes. Au site sableux, la germination carpogénique était corrélée négativement à un quotient de minéralisation du C et à une stabilité des agrégats plus élevés, alors que la germination était corrélée positivement avec la teneur en Ca. À l'opposé, la survie des sclérotes était corrélée négativement à la présence de Ca, alors que la survie était meilleure là où l'indice de fécondité du sol était plus élevé. La stabilité des agrégats et la teneur en Ca ont été favorisées par l'amendement en compost urbain qui n'a pas eu d'effet direct significatif sur la gravité de la maladie, mais était négativement corrélé à la survie et à la germination carpogénique des sclérotes. Les analyses de régression et d'ACR ont permis d'isoler des

variables clefs qui influencent la gravité de la maladie et ont contribué à expliquer leurs relations avec les pratiques culturales, la santé du sol et la variabilité spatiale des variables de la sclérotiniose. Cette analyse sera complétée au chapitre 3 par une partition de la variance des variables de sclérotiniose entre la variabilité spatiale, environnementale (couvert végétal, physico-chimie et microbiologie du sol) et la variabilité des traitements rotation et fertilisation.

Mots clés: *Sclerotinia sclerotiorum*, soja, indicateurs de santé du sol, stabilité des agrégats, minéralisation du C, comptages bactériens directs, analyse canonique des redondances.

Multivariate effects of plant canopy, soil physico-chemistry and microbiology on *Sclerotinia* stem rot of soybean in relation to crop rotation and urban compost amendment

Abstract: The effects of canopy, soil physico-chemical and microbiological variables on *Sclerotinia* stem rot (SSR) on soybean were assessed in two soils (clay loam and sandy loam) using multiple regression and canonical redundancy analysis (RDA) and their partial form to control for the rotation (2 or 3-y-corn/soybean monoculture) and fertilization (mineral/urban compost) or spatial variables effects. The models revealed the minimal sets of variables that best explain the variance of the survival of *S. sclerotiorum*'s sclerotia, carpogenic germination, disease severity and their associations. In clay loam, the 3-y-corn rotation reduced disease severity mainly through the reduction of weed biomass that favoured carpogenic germination. Urban compost has a conducive effect explained by a better soil surface drainage. Additionnally, total N was found suppressive to sclerotia survival. In sandy loam, the carpogenic germination was negatively correlated with high C mineralization quotient and aggregate stability but correlated positively with Ca. Sclerotia survival was negatively correlated with pH and Ca, and positively correlated with biological fertility index. Aggregate stability, Ca and pH were associated with the urban compost. The regression and RDA analyses allowed to identify key variables that drived SSR development and explain their relationship with the cultural practices, soil health, as well as the spatial variation of disease variables.

Key words : aggregates stability, C mineralization, canonical redundancy analysis, microbial direct counts, *Sclerotinia* stem rot, soil health indicators, soybean

Introduction

Sclerotinia stem rot (SSR) of soybean (*Glycine max* L.) is caused by the soil-borne discomycete *Sclerotinia sclerotiorum* (Lib.) de Bary. This disease which is distributed worldwide (Boland and Hall, 1994) has especially emerged in Northeastern America since the intensification of soybean production. In addition to the reduction of non-host crop rotation (Anderson, 1996), the use of irrigation (Grau and Radke, 1984) and the reduction of row spacing (Workneh et *al*., 1996) are also important contributors to SSR establishment. *Sclerotinia* stem rot is a disease with a large host range of mostly (herbaceous) dicotyledonous (Boland and Hall, 1994), including numerous weed species (Adams and Ayers, 1979).

Sclerotia are able to survive more than five years in the soil (Huang et *al.*, 1998). These structures consist of dense mycelium which is protected by melanized cortical cells (Willetts and Wong, 1980). This form of *S. sclerotiorum* affords the fungus longevity and resistance thus allowing it to attain a very high level of potential inoculum in infested fields. It further facilitates the initiation of a new disease cycle in susceptible crops even after 4 years of rotation with non-host crops (Schwartz and Steadman, 1978). These abilities of the disease agent are a threat to the development of soybean crops and they drastically reduce the number of alternative crops available to the growers.

Fungicides available in Canada for the reduction of SSR incidence are not economically viable for soybean growers (Kurle et *al*., 2001). The negative consequences of such chemical products for the environment and to public health have driven the search for alternative solutions for suppressing or reducing disease incidence under an economic threshold. These solutions often include cultural practices such as non-host crop rotation (Kurle et *al*., 2001; Mitchell and Wheeler, 1990) and reduced tillage or no-till (Garcia-Garza et *al*., 2002). The application of organic amendments, such as compost or solid manure in field (Asirifi et *al*., 1994) and liquid pork manure in greenhouse (Viana et *al*., 2000), has proven effective in reducing or suppressing *S. sclerotiorum* along with numerous soil-borne plant pathogens (Lazarovits, 2001). Other management practices such as wide row spacing (Workneh et *al*., 1996) and reduced irrigation (Grau and Radke, 1984) are currently used to lessen SSR severity. Antagonistic fungi of *S. sclerotiorum,* such as *Trichoderma harzianum* Rifai, have also been proposed to control the disease, but their effectiveness is often non persistent and varies with climatic and soil conditions (Lazarovits, 2001). Cultivars with early maturity,

reduced height, resistance to lodging, or cultivars with partial resistance (Cober et *al.*, 2003 ; Kurle et *al*., 2001; Rousseau et *al*., 2004) can be integrated in management practices to reduce the incidence of the disease and therefore, the amount of inoculum in infested fields. However, none of these integrated practices can efficiently control SSR individually or in a wide range of environments and soil conditions. Moreover, their modes of action are poorly understood and do not permit to accurately predict their potential to control *Sclerotinia* disease in soybean for a particular soil type or climatic condition.

The diversity and complexity of soil ecology, along with the lack of theoretical concepts that adequately describe the complex network of interactions of plants with soil as well as with their inhabitants, necessitate a more global approach in order to understand the agroecosystems. The objective of such an approach is to identify and to explain the links between soil health and ecosystem health (Rapport et *al*., 1997). Moreover, there is a need for a local approach which could identify, at the regional or field scale, the specificities of soils and plant canopy conditions that may contribute to the reduction of the disease incidence.

In the chapter 1 of this study, the effects of corn rotations and fertilization using urban compost on SSR variables, disease severity, carpogenic germination and sclerotia survival, were investigated in two soils. A wide range of physical and chemical characteristics were evaluated in the two soils in which this field experiment was performed (clay loam and sandy loam) (Chapter 1), along with microbiological variables, crop phenology and weed biomass (present Chapter 2). Meteorological data from the IRDA-CÉROM research station in Saint-Hyacinthe QC were also used for the interpretation of results (Chapter 1). To synthesize the effects of all these « environmental variables » (soil physico-chemistry and microbiology, crop phenology and weed biomass) on SSR disease variables, the canonical redundancy analysis (RDA) was used. RDA, and its partial form (pRDA), is a linear method of constrained canonical ordination, that allows the removal of spatial or treatment variation from the analyses (RDA and pRDA: van den Wollenberg, 1977). The *forward selection* procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002) was then used to reduce the set of environmental variables to the smallest set that best explains the SSR variables, controlling or not for spatial or treatment variation.

The first objective of this chapter 2 was to identify the environmental variables that best explain the variance in SSR disease variables, in order to construct minimal models including the most

parsimonious variables explaining SSR variables. The second objective was to investigate if the rotation and fertilization treatments enhance soil health as measured by the plant canopy and the soil physico-chemical and microbiological variables. The third objective aimed to identify the presence of a spatial structure in the disease variables. Methods have been proposed for exploring the spatial structure of ecological data and to include spatial location as a variable in the study of relationships and models in ecology (Borcard et *al.,* 1992 ; Legendre and Troussellier, 1988). To present knowledge, this approach has not yet been explored in the plant pathology literature. In this thesis, all the independent variables of the models that will be hypothesized to determine the variation in the SSR disease variables under study are called « environmental variables » (Borcard et *al.,* 1992): soil physico-chemistry and microbiology, crop phenology and weed biomass. The significant relationships between environmental and SSR variables can be spurious (false), implying a common gradient, while other relationships are real (Legendre and Troussellier, 1988). The relative contribution of each set of the environmental variables as well as the spatial structure of the variables which may explain the variance in the disease variables will also be detailed in Chapter 3.

Materials and Methods

The study site, field history, experimental design and disease assessments were detailed in the chapter 1. The canopy analyses (crop phenology and weeds), the soil and compost physico-chemical and microbiological analyses and the specific statistical analyses will be detailed in this chapter 2.

Experimental design

The experimental design was a split-plot with four blocks in which crop rotations consisted of the main plots and fertilizations the subplots. The rotation treatments were: 3-y-Corn = corn-corn-corn-soybean, 2-y-Corn = corn-corn-soybean-soybean, and a 4-y-soybean monoculture. The fertilization treatments were: NPK = mineral and UC = urban compost (Conporec inc., 2004). The study was conducted from 1999 to 2002 in two fields at the IRDA-CÉROM (Institut de Recherche et de Développement en Agroenvironnement; Centre de recherche sur les grains inc.) research station, in Saint-Hyacinthe (Québec, Canada) : a sand-clay loam site / Saint-Urbain series, and a sand to sandy-loam site / Saint-Damase series (Chapter 1).

Disease scoring

Sclerotinia stem rot of soybean was assessed by disease severity, carpogenic germination of sclerotia and sclerotia survival from 2000 to 2002. SSR disease severity was evaluated through the use of the disease severity index (DSI: Grau and Radke, 1984), by assessing carpogenic germination through counting apothecia produced by sclerotia applied on the soil surface, and by assessing sclerotia survival (firmness; van Toor et *al*., 2000) on shallow buried mesh bags after each growing season (Chapter 1).

Crop phenology

In 2000-2002, corn and soybean canopy was evaluated twice during the growing season (July and August) by measuring the Leaf Area Index (LAI) using a Plant Canopy Analyzer LAI-2000 by LI-Cor ®. LAI 1 at R2-R3 soybean stage (Full bloom-Beginning pod; Fehr et *al*., 1971) and LAI 2 at R5-R6 soybean stage (Beginning seed-Full seed). In 1999-2002, soybean yields (kg ha^{-1}) were measured by harvesting 40 m^2 per plot, with a Winstersteiger threshing-machine.

Weed monitoring

Weed populations were monitored in 2000-2002. All weeds were collected in two 1.5 m^2 quadrats per plot at soybean stage R7-R8: Beginning maturity-Full maturity. Roots were removed and weed dry matter was estimated by species for dicotyledonous, while for members of the graminaceae family, all species were pooled. In 2000, only one block per field was evaluated for weed populations. In 2001 and 2002, all the blocks were evaluated. Only the weed species that were present both years, in both soils, were included in the analysis.

Soil and urban compost analyses

Soil samples were analyzed for a range of standard physical and chemical parameters, in our laboratory or in a referenced soil analysis laboratory (Table 1). Samples for physical and chemical analyses were collected in the fields using a 5 cm diameter auger at depths of 0-10 cm and 10-20 cm. One sample was made of three subsamples collected within three 0.5 m^2 areas per plot in 1999 and two areas in 2000-2002. Samples were collected in July along a north-south diagonal in the experimental plots (see section « Analyses of soil and urban compost » in Chapter 1 for details).

Soil microbial activity

Soil microbial activity was measured on soil samples collected as described for physical and chemical analyses. For carbon mineralization quotient (CMQ) measurements, samples were collected in July, air dried, and sieved at 2.8 mm. The respiratory method was first developed by R. Schaefer (pers. com.) and described by Mboukou-Kimbatsa (1997). The respiratory method was applied to soil samples of the field plots, to a urban compost control and to an Ottawa Sand (S-23) control. This respiratory method measures the amount of CO_2 released from soil samples moistened at 80% of field capacity (Cassel and Nielsen, 1986), forced through a 2 mm sieve, and incubated (either 60 g for soil samples from field plots and Ottawa Sand control, or 25 g for urban compost control in hermetically sealed 250 mL erlenmeyer flasks), at 28°C in darkness, in Blue M Dry Type Bacterial incubators. The sealed erlenmeyer flasks were connected to the CO_2 trap system at day 2, 5, 14, 26 and 41 of incubation. The CO_2 from field soil samples, Ottawa Sand and urban compost controls, was extracted by vacuum (-2000 to -2500 kPa), trapped by barium hydroxide [$Ba(OH)_2$] solution and then titrated with oxalic acid. Carbon mineralization quotient (Dommergues, 1960) expressed the ratio CMQ = (C from CO_2 / soil total C)*100, where total soil C was determined by LECO CNS 2000 ® and all measures expressed for 100 g of dry soil. The originality of the respiratory method consists in complete CO_2 extraction from soil micropores by creating a -2000 to -2500 kPa depression in the system. The depression was applied twice for all samples. The atmosphere within each sample was then replaced by CO_2-free air, using an Ascarite II filter, after each depression. In this study, a modified version of the respiratory method described by Mboukou-Kimbatsa (1997) was used (Rousseau and Schaefer, 2003; Appendix A): 60 g instead of 150 g of soil samples were incubated ; glass tubes were replaced by 125 mL erlenmeyer flasks ; and tubes immersed in the alkali solution [$Ba(OH)_2$] were closed by pipette tips to ensure a regular diameter to the air bubbles.

For direct bacterial counts and Endo-C-agar CFU (colony forming units), soil samples collected in 1999 and 2002 with latex gloves from the 15th August to the 31st of August were homogenized, and kept at room temperature (20-22 ^{o}C), in the darkness. In less than 4 days of sampling, integrated techniques of direct bacterial counts and Endo-C-agar CFU were performed to evaluate soil biological fertility (from Rusch, 1972). A urban compost control was included in 1999 (Appendix B).

Two direct bacterial counts with Neubauer hemocytometer were performed. Ten g (20 g for urban compost control) of fresh field soil were mixed for 10 min at 250 rpm in a 250 mL erlenmeyer flask with 50 mL (100 mL for compost) containing either a physiological saline solution (7 gL^{-1} NaCl) (PS1) or a combination of this saline solution with 5 gL^{-1} Lactose and 5 gL^{-1} Dextrose (PS2). Field soil (or urban compost) suspensions were incubated aerobically for 48 h at 28°C in darkness, then filtered with a Wathman #1 filter paper. Filtration was stopped after 2 mL to prevent filter alteration and the suspension filtrate was directly counted with a Neubauer hemocytometer. Suspension filtrates were diluted as needed, particularly for urban compost control and PS2 suspensions. PS1 and PS2 suspensions were then plated on Endo-C-agar after counting. Endo-C-agar (Difco) plating medium selects lactic-acid-forming-bacteria (Lactobacteriaceae), which are revealed by a fuschin coloration. Fifty µL of PS1 and PS2 suspensions were plated on two compartments Endo-C-agar Petri dishes and incubated 48 h at 28°C in darkness. CFU1 and CFU2 were counted and sorted into three groups based on fuschin coloration and colony macromorphology. Group I, deep fuschin coloration; Group II, deep red coloration or pink coloration with deep red center; Group III, pink or reddish-black coloration, glair-forming-colonies, or any colonies that could not be classified in the first two groups. A biological fertility index (BFI) was calculated with the proportions of each group (pI, pII and pIII in %) in CFU1 + CFU2: BFI = ((pICFU1 + pICFU2) * 3) + (pIICFU1 + pIICFU2)) / (pIIICFU1 + pIIICFU2). Soil samples can be classified into four biological fertility groups according to BFI: BFI < 1, poor biological fertility (group III dominate); 1 < BFI < 5, moderate biological fertility; 5 < BFI < 20, good biological fertility; BFI > 20, very good biological fertility (group III rare to absent).

Statistical analyses

Univariate

Differences between the rotations (2-y-corn, 3-y-corn, 4-y-soybean), the fertilizations (mineral, urban compost) and their interactions were compared in each year for each environmental variable (phenology and weeds, physics, chemistry, microbiology) using analysis of variance (ANOVA) and a priori contrast comparisons where appropriate. ANOVAs were performed using the PROC GLM procedure of the Statistical Analysis System (SAS for Windows V8, SAS Institute Inc., 2001). Normality of data was tested using PROC CAPABILITY procedure of the Statistical Analysis System (SAS for Windows V8, SAS Institute Inc., 2001) and homogeneity of variances was examined by plotting residuals versus predicted values using the PROC GLM and PROC PLOT

procedures. Non-normal variables were previously transformed using appropriate transformations (Underwood, 1997).

Multivariate

Principal component analysis (PCA) was performed on all the environmental variables for each soil site in 2001 and 2002, to estimate the correlations between the environmental variables and the rotation and fertilization treatments (Legendre and Legendre, 1998). The PCA were performed with CANOCO 4.5 and correlation biplots with CanoDraw (Microcomputer Power, 2002). To assess the multivariate effects of environmental variables on SSR disease variables (DSI, apothecia number, sclerotia survival), and their combinations, multiple regression on single SSR variables and canonical redundancy analysis (RDA) on the combinations of SSR variables were performed. A first combination DSI-Apothecia was selected as the aerial matrix while a second combination, Apothecia-Survival, was defined as the soil matrix. Apothecia belong to both aerial and soil part of the agroecosystem as they emerge from sclerotia in soil. Apothecia forcibly discharge ascospores, the active inoculum leading to disease development.

RDA is an ordination method that can be considered as a multivariate extension of multiple linear regression. RDA is a principal component analysis modified to constrain the ordination axes to be linear combinations of a set of explanatory variables given in a separate matrix (Legendre and Legendre, 1998). To select the environmental variables that significantly explain or account for the SSR variables variance, the *forward selection* procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002) was done on each set of spatial variables and environmental variables : canopy (phenology and weeds), soil physics, chemistry and microbiology (Table 1). The matrix of spatial variables consisting of two-dimensional geographical coordinates, x and y measured in the center of each plot, was produced by adding all terms for a cubic trend surface regression of the form:

$$\hat{z}=b_1x+b_2y+b_3x^2+b_4y^2+b_5x^3+b_6y^3+b_7xy+b_8x^2y+b_9x^3y+b_{10}xy^2+b_{11}xy^3+b_{12}x^2y^2+b_{13}x^2y^3+b_{14}x^3y^3.$$

The 14 terms of the equation were submitted to the forward selection procedure as were the sets of environmental variables (Borcard et *al*., 1992). This first selection of variables was called the independent approach as the forward selection was computed independently on each set of variables. This first step was performed to keep the total number of variables under the threshold required by the analysis (df = number of samples - 1 = 23; Legendre and Legendre, 1998). Then, after the

reduction of the variable number in each set, the variables retained in each set were pooled and a second forward selection was performed on a unique global set. This second forward selection was called the additive approach (Pinel-Alloul et *al*., 1995). The additive approach provides a model containing the most parsimonious variables which explain the SSR disease variables variance (model I). The same analyses were repeated with the partial form of regression or RDA (pRDA) in order to control the treatments (rotation and fertilization) effects (model II), or the spatial variation (model III), when spatial variation or the treatments were significant. The set of spatial variables was created to estimate the extent of the spatial variation in the SSR variables (Borcard et *al*., 1992) and to detect spatial autocorrelation (Legendre and Trousselier, 1988).

As the two fields where the experiment was conducted were not homogeneous regarding soil type classification, a set of binary variables coding for soil type of each sample were added to the physical variables. Six binary soil type variables were created: sandy loam (SL), loamy sand (LS), sand-clay loam (SCL), sand-clay (SC), clay loam (CL) and clay soil (CS). All the soil variables (physics, chemistry and microbial activity) were labeled $_1$ when they were estimated in A_1 (0-10 cm), and labeled $_2$, when they were estimated in A_2 (10-20 cm).
The correlations between SSR variables and the environmental variables selected were represented in correlation triplots generated by CANODRAW (Microcomputer Power, 2002).

Results

Environmental variables

The ranges of the physical and chemical variables along with the ranges of soil microbiology variables in the clay loam and sandy loam field sites are presented in Table 1. According to the ANOVA analysis, Table 1 shows also the significant positive effects of rotation and fertilization treatments, soil depth, and their interactions on soil physico-chemistry and microbiology variables. Similarly, the ranges of SSR disease variables (DSI, sclerotia survival and carpogenic germination) and plant canopy (LAI, weed biomass and yields of soybean) are shown in Table 2. Again, the significant positive effects of rotation and fertilization treatments, soil depth, and their interactions on SSR and plant canopy variables are expressed according to the ANOVA analysis (Table 2).

Soil physico-chemistry

The mean weight diameter (MWD) was significantly higher in urban compost than in mineral fertilization plots in the clay loam site, in 2002, as well as in the sandy loam site in 1999 and 2002 ($P < 0.01$) (Table 1). The interaction A_1 x Urban Compost significantly enhanced organic matter content (OM) in the clay loam site, in 1999 and 2002 ($P < 0.05$) (Table 1). In sandy loam, the OM was significantly higher in urban compost than in NPK plots in 2002 ($P < 0.05$) (Table 1). The field capacity (FC) in the clay loam and sandy loam sites was significantly increased in A_1 x Urban Compost plots in 1999 ($P = 0.008$); FC was significantly higher in urban compost than in NPK plots in 1999 and 2002 ($P < 0.05$) (Table 1).

In both sites, the interaction A_1 x Urban Compost significantly enhanced pH in 1999 and 2002 (Table 1). The cation exchange capacity (CEC) in the clay loam site was significantly higher in A_1 in 1999 ($P = 0.002$), and in NPK plots in 2002 ($P < 0.0001$).

The A_1 x Urban Compost interaction effect was positively significant for the total C content (C) and N content (N) in the clay loam site in 1999 and 2002 ($P < 0.05$) (Table 1) ; whereas in sandy loam site, C and N were generally significantly higher in A_1 and in urban compost plots in 1999 and 2002 (Table 1). The C/N ratio was significantly higher in NPK plots in 2002 ($P < 0.0001$), and this, only in the sandy loam site (Table 1).

The total S content (S), in the clay loam site, was significantly higher in A_2 and in NPK plots in 1999 and 2002 ($P < 0.05$) (Table 1). In sandy loam, S was significantly higher in NPK than in urban compost plots in 2002 ($P = 0.04$) (Table 1).

The P, K, Ca and Al contents were regularly positively and significantly affected by fertilization or soil depth ; whereas, the Mg content (Mg) was significantly higher in urban compost plots, and this only in the sandy loam site, in 2002 ($P = 0.002$) (Table 1). The P concentration (P) in the clay loam site was significantly higher in A_1 in 1999 ($P = 0.008$), and in the urban compost plots in 2002 ($P = 0.003$) (Table 1). In the sandy loam, P was significantly higher in A_2 in 2002 ($P = 0.02$) (Table 1). The K concentration (K) in the clay loam site was significantly higher in A_1 in 1999 ($P < 0.0001$) ; an A_1 x Urban Compost interaction was positively significant for K content in 2002 ($P < 0.01$). In the sandy loam, K was significantly higher in A_1 and urban compost plots in 2002 ($P < 0.01$) (Table 1). The Ca concentration (Ca) in the clay loam site was significantly higher in A_1 and in urban

compost plots in 1999 ($P < 0.05$), and the A_1 x Urban Compost interaction was positively significant for Ca in 2002 ($P < 0.01$). In the sandy loam site, the interactions A_2 x NPK or A_1 x Urban Compost in 1999, and the urban compost plots in 2002 ($P < 0.01$) significantly increased the Ca content (Table 1). The Al concentration (Al) in the clay loam site was significantly higher in A_1 in 1999 ($P = 0.02$), and in A_2 and NPK plots in 2002 ($P < 0.01$) (Table 1). In the sandy loam site, Al was significantly higher in NPK plots in 2002 ($P < 0.05$) (Table 1).

Soil microbiology

The carbon mineralization quotient (CMQ) was enhanced in A_2 x Urban Compost compared with NPK x A_2 in the clay loam site, in 1999, at $P < 0.01$ (Table 1). The bacterial direct counts in PS1, in the sandy loam site, were significantly higher in 3-y-corn than in monoculture in 1999 ($P = 0.05$). In the sandy loam site, the 3-y-corn x NPK interaction had a greater effect than the 2-y-corn x NPK interaction on PS1, in 2002 ($P = 0.05$) (Table 1) ; the soybean Monoculture x Urban Compost interaction had a greater effect than the 3-y-corn x Urban Compost interaction on PS2, in 2002 ($P < 0.05$) (Table 1). The bacterial directs counts in PS2 in the clay loam site were significantly higher in soil depth A_1 than A_2 in 2002 ($P = 0.05$) (Table 1). In the sandy loam in 2002, the biological fertility index (BFI) was significantly higher in Monoculture x NPK compared with the 3-y-corn x NPK interaction (Table 1).

Sclerotinia stem rot variables

The DSI disease index was significantly and positively affected in clay loam site by urban compost in 2001 and by 2-y-corn rotation/soybean monoculture in 2002 (Table 2). In the sandy loam site the interactions soybean monoculture x NPK and 3-y-corn rotation x Urban Compost had a significant negative effect on DSI in 2001 and 2002, respectively (Table 2). However, carpogenic germination was not significantly affected while urban compost amendment had a significant positive effect on sclerotia survival only in the clay loam site in 2001 (Table 2).

Plant canopy

There was a positive significant effect of the interaction 3-y-corn x Urban Compost for the LAI at R2-R3 soybean stage (LAI1) in the clay loam site, in 2002 ($P < 0.05$) (Table 2). The LAI at R5-R6 soybean stage (LAI2) in the sandy loam was significantly and positively affected by Monoculture x Urban Compost in 2001 ($P < 0.001$) (Table 2). The soybean yields (Yield) in the clay loam site was

significantly higher in 2-y-corn rotation compared with soybean monoculture in 2001. A positive significant effect of the interaction 3-y-corn x Urban Compost for soybean yields was noticed in the clay loam site, in 2002 ($P < 0.05$) (Table 2). In the sandy loam, Yield was significantly higher following the 3-y-corn rotation (in 2002 ; $P = 0.0004$) (Table 2).

Ambrosia artemisiifolia was the main weed species in both sites, in 2001 and 2002. The second prevailing dicotyledon species was *Chenopodium album*. Moreover, the mean biomass of the dicotyledons was twice as much as the monocotyledon biomass (Table 2). In both sites, in 2001, there was a positive significant effect of the interaction Monoculture x Urban Compost for *A. artemisiifolia* biomass ; in 2002, *A. artemisiifolia* biomass was higher in soybean monoculture and urban compost plots. *C. album* was favored by NPK fertilization in both sites in 2001. Total weed biomass and dicotyledons biomass were mostly associated with soybean monoculture and Urban Compost plots (Table 2).

Principal component analysis (PCA)

The correlations of soil and canopy variables were illustrated with the use of PCA biplots which were performed for each soil site in 2001 and 2002. The PCA biplots are presented in Figs 1 (a-b) for the clay loam and Figs 2 (a-b) for the sandy loam sites. The first two PCA axes in clay loam explained 22.4% (22.7%) and 15.2% (17.6%) respectively in 2001 (2002) of the variance in the environmental variables. In sandy loam, the first two PCA axes explained 15.8% (21.5%) and 12.8% (16.0%) respectively in 2001 (2002) of the variance in the environmental variables. In 2001-2002, in the clay loam and sandy loam sites (Fig. 1a-b; Fig. 2a-b), all PCA biplots indicated positive correlation between field capacity (FC), OM, mean weight diameter (MWD), three selected physical and chemical properties, and Urban Compost amendment (fertilization treatment). Two of the negative correlations systematically observed in all four PCA biplots were between sand and clay, and between Urban Compost and NPK fertilization treatments (Figs 1 and 2).

In the clay loam site, in 2002, the first component axis of PCA biplots was correlated to (and opposed to) sand and clay ; the second component axis was correlated to Urban Compost and NPK (Fig.1a). In the clay loam site, in 2001, the first principal component axis was correlated to (and opposed to) Urban Compost and NPK fertilization treatments (Fig. 1b). In the sandy loam site, in 2002, the first component axis of PCA biplots was negatively correlated to bacterial direct counts (PS1 and 2); the second component axis being related to (and opposing) Urban Compost and NPK

(Fig. 2a). In the sandy loam site, in 2001, the first principal component axis was positively correlated to field capacity (FC), OM, and mean weight diameter (MWD) (Fig. 2b), the second component axis being related to (and opposing) Urban Compost and NPK. This results in a separation of the fertilization (NPK / Urban Compost) treatments on the one hand, and of clay and sand on the other hand.

Multiple regression analyses on individual SSR variables

Multiple and partial regression analyses were performed on each of the *Sclerotinia* stem rot variables : disease severity index (DSI), carpogenic germination (Apothecia) and sclerotia survival (Survival). An additive approach was first used (model I) that included all environmental variables that have been previously selected using forward selection on each set of environmental variables (independent approach; Pinel-Alloul et *al*., 1995). A partial regression was then performed to control for treatments (model II) or space (variables previously selected by forward selection on all spatial variables: model III), if their effects were significant.

Disease severity (DSI)

In the clay loam site, a multiple regression on DSI revealed a model explaining 80.5% of DSI variation, a model that retained five variables (model I, $P = 0.001$) (Table 3). In model I, the regression axis was positively correlated with S_2 ($r^2 = 0.08$) as well as with $PS1_2$ ($r^2 = 0.06$), while it was negatively correlated with Yield ($r^2 = 0.51$) and $Silt_2$ ($r^2 = 0.08$) (Table 3). The partial model II, which controlled for rotation, explained 34.2% of DSI variation, and retained only two variables ($P = 0.002$). The partial regression axis was positively correlated with $Silt_2$ ($r^2 = 0.20$), and negatively with S_2 ($r^2 = 0.14$) (Table 3).

In the sandy loam site, the additive model I retained three variables that explained 45.2% of DSI variance ($P = 0.008$) (Table 3). In model I, the axis was correlated positively with OM_2 ($r^2 = 0.11$) and negatively with Total weed ($r^2 = 0.24$) and *Amaranthus retroflexus* ($r^2 = 0.10$) (Table 3). The partial model II, controlling for the rotation x fertilization interaction, explained 38.3% of DSI variance and retained two variables ($P = 0.004$). Total weed biomass ($r^2 = 0.30$) was positively correlated with model II axis, and negatively with C_1 ($r^2 = 0.08$) (Table 3). The partial regression model III, which controlled for spatial variation, explained 19.1% of DSI variance, while retaining

two variables ($P = 0.017$). The axis was correlated positively with P_2 ($r^2 = 0.09$), and negatively with CEC_2 ($r^2 = 0.10$) (Table 3).

Carpogenic germination (Apothecia)

In the clay loam site, a multiple regression on Apothecia revealed that a five variable model explained 82.9% of Apothecia variance (model I, $P = 0.001$) (Table 4). In model I, the axis was positively correlated with Total dicotyledons ($r^2 = 0.20$), $PS1_1$ ($r^2 = 0.03$), and CS_2 ($r^2 = 0.13$), while it was negatively correlated with P_2 ($r^2 = 0.37$) and Al_2 ($r^2 = 0.10$) (Table 4). The partial regression model III, controlling for spatial variables, explained only 8.9% of the variance in Apothecia while retaining three variables ($P = 0.001$). The variables Total dicotyledons ($r^2 = 0.04$) and CS_2 ($r^2 = 0.03$) were correlated positively with model III axis, and MWD ($r^2 = 0.02$) negatively (Table 4).

In the sandy loam site, the model I retained four variables that explained 70.4% of carpogenic germination (Apothecia) variance ($P = 0.001$) (Table 4). In model I, the axis was positively correlated with $Clay_1$ ($r^2 = 0.35$) and *Ambrosia artemisiifolia* ($r^2 = 0.09$). It was also negatively correlated with CMQ_1 ($r^2 = 0.08$) and MWD ($r^2 = 0.18$) (Table 4). The partial regression model III, which controlled for spatial variation, explained 55.1% of Apothecia variance while retaining six variables ($P = 0.002$). *A. artemisiifolia* ($r^2 = 0.13$) and $Clay_1$ ($r^2 = 0.08$) were positively correlated with the axis, while CMQ_1 ($r^2 = 0.15$), MWD ($r^2 = 0.09$), Al_2 ($r^2 = 0.06$) and Al_1 ($r^2 = 0.04$) were negatively correlated (Table 4).

Sclerotia survival (Survival)

In the clay loam site, a multiple regression on Survival revealed a four variable model explaining 78.5% of sclerotia survival variation (model I, $P = 0.001$) (Table 5). In model I, the axis was positively correlated with *Polygonum aviculare* ($r^2 = 0.11$), $Sand_1$ ($r^2 = 0.11$) and $Clay_2$ ($r^2 = 0.17$). However, it was negatively correlated with N_2 ($r^2 = 0.40$) (Table 5). The partial regression model III, which controlled for spatial variation, explained 11% of Survival variance while retaining only two variables ($P = 0.015$). The axis was negatively correlated with N_2 ($r^2 = 0.07$) and Total dicotyledons ($r^2 = 0.04$) (Table 5).

In the sandy loam site, model I retained three variables which explained 51.5% of Survival variance ($P = 0.001$) (Table 5). The axis was positively correlated with BFI_1 ($r^2 = 0.20$). It was also negatively correlated with pH_1 ($r^2 = 0.14$) and P_1 ($r^2 = 0.17$) (Table 5). The partial regression model II, which

controlled for rotation effect, explained 43.4% of sclerotia survival variance while retaining the same three variables. The axis remained positively correlated with BFI_1 ($r^2 = 0.11$). It was also negatively correlated with pH_1 ($r^2 = 0.22$) and P_1 ($r^2 = 0.10$) (Table 5).

Redundancy analyses on DSI-Apothecia and Apothecia-Survival matrices

Redundancy and partial redundancy analyses (RDA and pRDA) were performed on the matrices formed by the association of DSI and Apothecia or of Apothecia and Survival. The first association was considered as the « aerial » matrix while the second was considered as the « soil » matrix.

The aerial matrix: disease severity and carpogenic germination

In the clay loam site, the DSI was slightly correlated with Apothecia (r = 0.37, *P* = 0.06). Model I explained 65.4% of the variability in the DSI-Apothecia matrix, and retained four variables (*P* = 0.001) (Table 6). In model I, the first RDA axis (RDA I) explained 54.1% of the variability in DSI-Apothecia and was positively correlated with DSI and Apothecia (Fig. 3a). RDA I was positively correlated with Total dicotyledons ($r^2 = 0.41$), $PS1_1$ ($r^2 = 0.05$), and *P. aviculare* ($r^2 = 0.06$) and was negatively correlated with P_2 ($r^2 = 0.13$). The second RDA axis (RDA II) explained 13.3% of the variability in the DSI-Apothecia, and was positively correlated with the DSI and negatively with Apothecia. RDA II was positively correlated with the P_2 and Total dicotyledons but was negatively correlated with *P. aviculare* (Fig. 3a). In model II, pRDA which controlled for rotation (fertilization) effects, the total variance accounted for by the model was of 48.6 (59.7)%. As in model I, the four same variables were retained in this analysis (*P* = 0.001) (Table 6). The first pRDA axis (pRDA I) [eigenvalue = 0.44 (0.48)] (triplot not shown) was positively correlated with DSI and Apothecia. Total dicotyledons [$r^2 = 0.26$ (0.33)], $PS1_1$ [$r^2 = 0.06$ (0.05)] and *P. aviculare* were correlated positively with pRDA I. This same axis was negatively correlated with P_2 [$r^2 = 0.10$ (0.13)]. The second pRDA axis (pRDA II) [eigenvalue = 0.05 (0.12)] was positively correlated with DSI and negatively with Apothecia. P_2 (*P. aviculare*), $PS1_1$ and Total dicotyledons were positively correlated with pRDA II, and *P. aviculare* (P_2 and Total dicotyledons) was negatively correlated with this axis. In model III, pRDA which controlled for spatial variation, the total variance explained by this model dropped by 21.5%. This model III retained two variables (*P* = 0.001) (Table 6). The pRDA I (eigenvalue = 0.20) was positively correlated with DSI and Apothecia (Fig. 3b). Total dicotyledons ($r^2 = 0.18$) were positively correlated with pRDA I, and $Silt_2$ ($r^2 = 0.04$) was negatively correlated with this axis. Both environmental variables were negatively correlated with pRDA II (eigenvalue = 0.02) (Fig. 3b).

In the sandy loam site, the DSI and Apothecia were uncorrelated (r = 0.21, $P > 0.1$). Model I explained 59.2% of DSI-Apothecia matrix and retained five variables ($P = 0.001$) (Table 6). The interaction of rotation with fertilization was also significant (Table 6). In model I, RDA I (eigenvalue = 0.43) was positively correlated with DSI and Apothecia (Fig. 4a). *A. artemisiifolia* ($r^2 = 0.24$) and $Clay_1$ ($r^2 = 0.06$) were positively correlated with RDA I, and MWD ($r^2 = 0.08$) was negatively correlated with this axis. The RDA II (eigenvalue = 0.16) was positively correlated with the DSI and negatively correlated with Apothecia. CMQ_1 ($r^2 = 0.13$) was positively correlated with RDA II, SL_2 ($r^2 = 0.08$) and $Clay_1$ were negatively correlated with this axis (Fig. 4a). In model II of the pRDA which controlled for the effect of the rotation x fertilization interaction, the total variance explained was of 43.7%. In this model, three variables were retained ($P = 0.002$) (Table 6). The pRDA I (eigenvalue = 0.30) was positively correlated with DSI and Apothecia (triplot not shown). *A. artemisiifolia* ($r^2 = 0.25$) and SL_2 ($r^2 = 0.07$) were positively correlated with pRDA I, and CMQ_1 ($r^2 = 0.12$) was negatively correlated with this axis. The pRDA II (eigenvalue = 0.14) was positively correlated with DSI and negatively correlated with Apothecia. CMQ_1 and *A. artemisiifolia* were positively correlated with pRDA II while SL_2 was negatively correlated with this axis. In model III, pRDA which controlled for spatial variation, the total variance explained was of 21.8%. In this analysis, two variables were retained ($P = 0.011$) (Table 6). The pRDA I (eigenvalue = 0.14) was positively correlated with the DSI and negatively correlated with Apothecia (Fig. 4b). The pRDA I was negatively correlated with *A. artemisiifolia* ($r^2 = 0.12$), and positively correlated with CMQ_1 ($r^2 = 0.10$). The pRDA II (eigenvalue = 0.07) was positively correlated with DSI, Apothecia, as well as with all environmental variables (Fig. 4b).

The soil matrix: carpogenic germination and sclerotia survival

In the clay loam site, Apothecia and Survival were positively correlated (r = 0.71, $P = 0.003$). Model I explained 71.8% of the Apothecia-Survival matrix. This model retained five variables ($P = 0.001$) (Table 7). In model I, RDA I (eigenvalue = 0.66) was positively correlated with Apothecia and Survival (Fig. 5a). Total dicotyledons ($r^2 = 0.06$) and *P. aviculare* ($r^2 = 0.05$) were positively correlated with RDA I while P_2 ($r^2 = 0.35$), CL_2 ($r^2 = 0.21$) and $Clay_1$ ($r^2 = 0.05$) were negatively correlated with this axis. The RDA II (eigenvalue = 0.06) was positively correlated with Apothecia and negatively correlated with Survival. Total dicotyledons and $Clay_1$ were also positively correlated with RDA II, while *P. aviculare* was negatively correlated with this axis (Fig. 5a). In model III, the pRDA which controlled for spatial variation, the total variance explained dropped to

7.6%. In this model, only two variables were retained (P = 0.008) (Table 7). The pRDA I (eigenvalue = 0.07) was positively correlated with Survival and negatively with Apothecia (Fig. 5b). N_2 (r^2 = 0.04) and Total dicotyledons (r^2 = 0.04) were negatively correlated with pRDA I. The pRDA II (eigenvalue = 0.01) was positively correlated with Apothecia and Survival. The pRDA II was positively correlated with Total dicotyledons and negatively correlated with N_2 (Fig. 5b).

In the sandy loam site, Apothecia and Survival were not correlated (r = 0.08, P > 0.05). Model I explained 49.1% of the Apothecia-Survival matrix and retained three variables (P = 0.001) (Table 7). In model I, the RDA I (eigenvalue = 0.30) was positively correlated with Survival and negatively correlated with Apothecia (Fig. 6a). CMQ_1 (r^2 = 0.16) and BFI_2 (r^2 = 0.09) were positively correlated with RDA I, while *A. artemisiifolia* (r^2 = 0.24) was negatively correlated with this axis. The RDA II (eigenvalue = 0.19) was positively correlated with Survival and Apothecia, as well as with all environmental variables (Fig. 6a). In model III, pRDA, which controlled for spatial variation, explained 38.3% of the observed variance. In this model, the three variables mentionned were retained (P = 0.001) (Table 7). The pRDA I (eigenvalue = 0.24) was negatively correlated with Survival and Apothecia (Fig. 6b). The pRDA I was positively correlated with Ca_1 (r^2 = 0.14) and negatively correlated with *A. artemisiifolia* (r^2 = 0.16) and CMQ_1 (r^2 = 0.08). The pRDA II (eigenvalue = 0.14) was positively correlated with Suvival and negatively with Apothecia. The pRDA II was positively correlated with CMQ_1 and *A. artemisiifolia* but was negatively correlated with Ca_1 (Fig. 6b).

Discussion

Environmental variables as indicators of soil health

One objective of this study was to determine if the treatments (rotation with corn and organic fertilization) had a positive effect on soil health. Regarding this effect, this research aimed to identify the relations with SSR under the hypothesis that enhanced soil health would be able to reduce the severity of the SSR disease. Among the soil and agroecosystem variables estimated, this discussion will focus on those previously recognized as useful soil health indicators and discuss their evolution during the experiment regarding the effects of treatments and differences between sites.

Basically, Rapport et *al*. (1997) defined two intersecting sets of indicators of soil health: those related to productivity and those related to soil ecology. Soil structure, estimated by aggregate stability, as indirect indicator of the influence of soil biota on other parts of the system (Karlen and Stott, 1994), may be the most useful in assessing soil health (Rapport et *al*., 1997), even if aggregate stability is difficult to estimate in a single, consistantly meaningful way (Kay, 1990). Soil aggregate stability was estimated by mean weight diameter (Kemper and Rosenau, 1986). Soil OM content and field capacity (Cassel and Nielsen, 1986), which may help to interpret changes in the soil physical characteristics, were also estimated. As shown in Table 1, these three properties were enhanced by the urban compost fertilization in both soils, and are well correlated to each other (Fig. 1a-b; Fig. 2a-b). This confirmed the hypothesis that stated the beneficial impact of OM in the form of urban compost amendment on the soil physical characteristics, i.e. wet aggregate stability and water holding capacity.

Chemical variables such as pH, CEC or major nutrient concentrations may change quickly in response to soil management, and then may be relevant indicators for both soil quality and soil health (Pankhurst et *al*., 1997). Most of the chemical parameters evaluated were enhanced by compost amendment, except S and Al which were enhanced by mineral fertilization in both soils (Table 1). So, the effect of organic fertilization can be considered as positive concerning soil health, whereas the effect of mineral fertilization would be neutral or negative, as S and Al are potentially phytotoxic (Rapport et *al*., 1997). The C/N ratio was significantly enhanced only in mineral fertilization in the sandy loam in 2002. This C/N ratio rise was related to the total C and N increase in compost-amended plots where the total N concentration may decrease less quickly than in mineral-fertilized plots, possibly because of the highest proportion of organic forms of N (more resistant to degradation) and higher OM content, that may prevent leaching of nutrients caused by low CEC and water holding capacity, particularly in sandy loam (Lamontagne, 1991).

The soil respiration is a well established parameter to monitor decomposition of OM in soils (Anderson, 1982), but it is also highly variable depending on substrate availability, moisture or temperature (Fließbach et *al*., 1994). So, under conditions where moisture and temperature are controlled and not limiting, the rate of CO_2 flow can provide an indication of OM quality and whether the soil environment is conducive to decomposition processes (Sparling, 1997). One of the most used indicator of soil respiration is the respiratory quotient (qCO_2) defined as the ratio of CO_2-

C mineralized from C of microbial biomass (Anderson and Domsch, 1989). In Anderson and Domsch (1989) method, the C of biomass is determined by the SIR method (Substrate Induced Respiration) of Anderson and Domsch (1978). As the induced respiration is able to change from one soil to another (Jenkinson et *al*., 2004) and because this method was not tested on the soils of this study, a method measuring the C mineralization quotient (CMQ) was adopted as described in the method section (Dommergues, 1960; Rousseau and Schaefer, 2003/Appendix A). Indeed, this quotient is based on the ratio of CO_2-C / total C, and therefore was not subjected to the variations that could be encountered in the SIR method.

In the two soils tested in the present study, the CMQ was low. This is generally the case for the mineral soils poor in OM (Bachelier, 1968). Soils were different regarding the CMQ in 2002, the clay loam supported an higher rate of C mineralization than the sandy loam. This difference was significant and increased from 2000 to 2002 (data not shown). As sandy soils support generally an higher metabolic rate than clay soils, these results may be surprising. However, during the study, the weather was dryer than the 30-y-normals, with year 2002 being the driest during the sampling time (July-August) (Chapter 1; Appendix D). The estimations of field capacity and wet aggregate stability confirmed the potential of clay loam to support an higher microbial activity under dry conditions. As stated by Dommergues (1960) and Bachelier (1968), the CMQ was usefull to differentiate the global biological activity of two soil types.

The qCO_2 (Anderson and Domsch, 1989; 1990) was reported to be lower in the mature or more complex ecosystems, compared with younger ones. In particular, the qCO_2 was found lower in soils under crop rotation compared with soils under monoculture. This was consistent with the Odum's theory on bioenergetics (Odum, 1969) which stated that more the ecosystems are closed to climax, higher is the yield of energetic processes. That is to say, the highest biodiversity and species interactions allow the highest efficiency in the use of available C sources (Fließbach and Mäder, 1997). By comparison, higher CMQ may be explained by a better energetic yield or a higher microbial biomass, or both. As direct bacterial counts were found proportionnal with microbial biomass (Jenkinson et *al*., 1976), the results of soil respiration are discussed jointly with the bacterial direct counts.

In clay loam, it was hypothesized that the opposite effect of fertilization according to rotation on CMQ in 2000-2001 (data not shown) was due to the rhizosphere-induced microbial biomass. That is

to say that the highest rhizodeposition by corn in compost-amended plots might allowed the development of more microbial activity, and possibly diversity, than in soybean (Kuzyakov, 2002). In the presence of compost, corn, which needs high nutrient levels, has to provide more energy to the microorganisms to enhance the availability of nutrients through the degradation of OM, and then balance the deficit in available nutrients, N particularly. In soybean, a deficit was not expected in available nutrients in compost-amended plots as previously noticed with urban compost of the same origin (M. Laverdière, pers. com.). So, the soybean rhizosphere was probably characterized by lower rhizodeposition, compared with corn. This could explain why the CMQ remained lower in soybean plots with compost in 2000-2001, but was enhanced by the presence of mineral amendment providing available nutrient for the development of microbial biomass and activity. Additionally, mineral fertilization was reported to reduce rhizodeposition and enhance OM mineralization (Warembourg and Estelrich, 2001). The absence of effects in 2002, where all plots returned to soybean, supports the hypothesis of a strong specific interaction between corn and compost. The 2001 results of bacterial counts and BFI in clay loam did not reveal any interaction of corn with compost, although the BFI was higher in corn compared with soybean (only in 2-y-corn plots). This suggested a positive effect of corn on the presence of root symbionts. This was confirmed in sandy loam in 2001, where BFI was higher in corn than in soybean.

To summary, it is hypothesized that in the presence of urban compost, corn reacted by enhancing rhizodeposition, leading to higher CMQ or BFI, while soybean reacted more to mineral fertilization, possibly by lower rhizodeposition, but also by a higher C mineralization rate that was stimulated by available N provided by fertilization and soybean roots.

In 2002, the BFI in sandy loam showed the same opposition in the effects of fertilization as for CMQ in clay in 2001 (data not shown). This may be explained by the persistence of the microbial community promoted by the interaction of rotation with fertilization. In 2001, the BFI was higher in corn supporting the effect of rhizodeposition by corn (data not shown). However, the bacterial counts in 2002 showed an opposite trend in response to the same interaction (Table 1). This might be explained by the contrasted susceptibility of the bacterial counts and BFI to the variation in OM induced by the treatments. The BFI was assumed to be indicative of rhizosphere priming effects (RPE; Kuzyakov, 2002) induced by rhizodeposition while the bacterial counts seem to be more indicative of priming effects (PE; Kuzyakov et *al*., 2000) that characterizes bulk soil. A PE is a short term change in the turnover intensity of soil OM caused by different factors such as fertilization,

plant cultivation etc. In the case of plant cultivation, PE occurs in the direct vicinity of living roots, therefore it is called RPE (Kuzyakov, 2002). In 2002, direct bacterial counts (PS1) were higher in 3-y-corn x NPK suggesting a stimulation of bacterial abundance by the presence of the corn residues and inorganic N that allowed a positive PE. In the compost-amended plots, where N is probably less available, the PS2 bacterial counts were higher in the monoculture and 2-y-corn, suggesting that soybean-released N allowed a positive PE (Table 1).

Whereas the physical and chemical variables showed a clear response to the fertilization and a clear trend of enhanced soil health resulting from compost application, the microbial variables proved to be more sensitive to the interaction of rotation with fertilization, as well as to soil depth. As a consequence, it was not possible yet to clearly state that the rotation and fertilization treatments enhanced the biological fertility of the soils. These results are consistent with the conclusions of most authors who studied the microbial activity or biomass as indicators of soil health. Up to date, the knowledge of soil ecosystems is not sufficient to use or recommend biological indicators as routine tools to monitor soil health (Rapport et *al*., 1997). However, microbial indicators are probably useful to measure changes resulting from some perturbations (degradation or rehabilitation), but it is essential to have controls which are subjected to the same treatments and remain free from the perturbation under study (Roper and Ophel-Keller, 1997). Thus, the methods used in this study have a potential for longer term study, by comparison with qCO_2 developped by Anderson and Domsch (1990), and more investigations are needed to interpret the results and enhance their precision and use. However, the combination of CMQ and direct counts/BFI appeared reliable to identify and explain the variations of soil OM decomposition induced by the interaction of the crops with fertilization, and attributed to RPE and PE, as hypothesized by Kuzyakov (2002) and Kuzyakov et *al*. (2000).

The yields or plant biomass are considered as bioindicator of soil health, decreasing yields or plant biomass indicating loss of health (Powlson and Johnston, 1994). In this perspective, high yields may indicate soil health and constant or increasing yields would indicate conservation or enhancement of soil health. In both soils, the soybean yield was better in rotations in 2002 (Table 2). It may then be concluded that rotations were conducive for better soil health as indicated by soybean yield. The compost affected the yield only in interaction with rotation, and as previously noticed, it induced N deficiency in the corn crop at the beginning of the experiment. Therefore, the compost was poorly associated with soil health as indicated by corn yields (data not shown). The interaction of weed

biomass with yield, disease, and treatments will be discussed in the following sections of this chapter 2. However, it is noticed that despite this opposite effect of treatments on monocotyledons and dicotyledons (Table 2), the total weed biomass was enhanced by the interaction of monoculture and compost, suggesting that compost created better soil conditions for weed development. This is consistent with the positive effects of compost on soil physico-chemical characteristics already noticed. The use of rotation as a method for integrated weed control compared with monoculture was well documented, and easily explains the trend of rotation effect on weed and soybean yield. Indeed, by the introduction of diversity and variability in crop cover, the rotation is less favorable to the weed adaptation and performance compared with monoculture (Kremer and Li, 2003).

Multiple regression analyses on individual SSR variables

In the clay loam site, the reduction of DSI by corn rotation (Chapter 3) contributed to better yields and may explain why the regression model I attributed most of the DSI variation to the yield. Actually, DSI explained the soybean yield which was enhanced by DSI reduction as well as by a weed biomass reduction in the 3-y-corn x Urban Compost compared with Monoculture x Urban Compost (Table 2). Moreover, where the weed biomass was higher, the soybean was probably more etiolated and therefore more susceptible to the infection by *S. sclerotiorum* (Cline et Jacobsen, 1983). When controlling for rotation effect (model II), the explained variance dropped and Yield was no more included (Table 3). This confirmed the association of Yield with the 3-y-corn rotation (the effect of compost was not removed from this analysis). In the model I, S_2 was found positively correlated with DSI but its contribution was lower than in model II. This contradiction might be explained by the negative correlation of S_2 with the yield previously included in the model, as well as by its association with the 2-y-corn rotation, as shown in the PCA in 2002 and 2001 (Fig. 1a-b). The sulfur is one of the oldest and widely used fungicide, as pure sulfur or in sulfurous molecules as isothiocyanates (Ware, 2000). Natural isothiocyanates from *Brassica* sp. are potential alternatives to synthetic formulations for biofumigation to control a wide variety of plant pests (Morra and Kirkegaard, 2002). Isothiocyanates were also reported to be suppressive against *Sclerotinia minor* through incorporation of broccoli tissues (*Brassica oleracea* L. var. *botrytis* L.) in rotation with lettuce (Hao et *al*., 2003). Moreover, SO_4 was already reported to stimulate antibiosis in the rhizosphere (Sturz et *al*., 2004), where the antibiosis was attributed mainly to *Bacillus* sp. already noticed as *S. sclerotiorum* antagonist (Viana et *al*., 2000). As a consequence, S is likely to have a suppressive effect against SSR on soybean. In the present case, two phenomena may have occurred: 1) isothiocyanates or volatile S-coumpounds involved in suppression required transformation in the

soil to be released or activated (Morra and Kirkegaard, 2002); 2) the S-compounds became protective in soybean plants after S mineralization and absorption (Goh and Pamidi, 2003). The first hypothesis could explain why S_2 was not correlated with *B. kaber* (Fig. 1b) and why only S in A_2 showed suppressive effect (Table 3). The second hypothesis could explain why S was not included in the models including Apothecia or Survival (Table 4 to 7). $Silt_2$ was well correlated with DSI in model II (Table 3). The contradiction with model I may be explained by the positive correlation of $Silt_2$ with LAI1 and Yield, previously included in the model. Then, the conducive effect observed in model II can be explained, in a fine textured soil such as clay loam, by the better conditions of stipe emergence to form apothecia, and therefore higher apothecia number and diameter, as previously reported for corser textured soils as silt loams (Kurle et *al*., 2001; Mueller et *al*., 2002) or sandy loams (Singh and Tripathi, 1996). This relation between carpogenic germination and disease severity will be discussed in the multivariate section.

In the sandy loam site, the presence of dense weed canopy was conducive for SSR because of microclimatic effects which created higher humidity and reduced temperature under canopy (Grau and Radke, 1984; Teo et *al*., 1989). The weeds can also become a source of inoculum as most of dicotyledons are susceptible to SSR (Boland and Hall, 1994). This inoculum can be constituted by sclerotia produced on weeds in previous years or mycelium that was already observed to infect soybean by contact (Rousseau et *al*., 2004). In this soil, the compost tended to reduce the weed biomass in 3-y-corn compared with monoculture (Table 2). This weed biomass reduction may have contributed to the disease severity reduction. C content may affect disease severity by the reduction of sclerotia survival or carpogenic germination (Asirifi et *al*., 1994). The humic substances were also reported to stimulate soybean dry matter production, nodulation and nodules N content (Tan and Tantiwiramanond, 1983) and therefore may enhance soybean resistance to SSR. The model I of multiple regression showed DSI correlated positively with OM_2, and negatively with weed biomass. This contradiction with model II shows an interaction between these variables and the 3-y-corn x Urban Compost interaction. Indeed, the model I reflects the correlations between the variables and 3-y-corn x Urban Compost: the weed variables are negatively correlated with 3-y-corn rotation and urban compost while OM_2 was correlated with urban compost. Then, the model I seems to explain the variation in DSI induced by the interaction. In model III controlling for space no weed variable was included anymore (Table 3), which showed an interaction of weed effect with spatial structure of disease development, i.e. where the weed canopy is denser the microclimatic conditions are conducive for disease development (Grau and Radke, 1984). Therefore, the weeds may not have

directly affected the disease severity as an inoculum source but their effect was rather indirect, acting through the climatic conditions. The CEC_2 and P_2 chemical variables appeared in the model III. These variables appeared to be more clearly linked to carpogenic germination or sclerotia survival than to DSI directly, therefore their effects will be discussed in the following sections.

In the clay loam site, the weed biomass was conducive for carpogenic germination (Table 4), as already discussed for disease severity. Higher clay content was also associated with more apothecia, this was attributed to the conservation of moisture under the dry conditions that prevailed during the experiment, particularly in 2002 (Chapter 1). P_2 and Al_2 seem to have an inhibitory effect on carpogenic germination according to model I (Table 4). The effects of phosphate that were reported to protect plants against the powdery mildew fungus (*Blumeria graminis* f. sp. *hordei* Marchal) were attributed to systemic acquired resistance (Mitchell et Walters, 2004), while the direct effects of phosphite (potassium phosphonate) on *Phytophthora cinnamomi* were not demonstrated (Barrett et *al*., 2003). Additionally, P_2 was reported to be positively correlated with DSI in model III on sandy loam (Table 3). Therefore, more investigations are needed to confirm the inhibitory effect of P on carpogenic germination. According to model III, most of the Apothecia variation was spatially structured (Table 4). The exclusion of P_2 and Al_2 in model III suggests that they shared a common spatial structure with Apothecia, but no real causal relation. The MWD diameter, which estimated the wet aggregates stability, was already reported as a possible suppressive factor for *Sclerotinia minor*'s sclerotia (Tokeshi et *al.*, 1997). Indeed, higher structural stability enhances soil drainage and aeration which lead to a reduction of water potential at soil surface (Kay and Angers, 1999) and a higher biological activity which may inhibit sclerotia survival or carpogenic germination, as suggested by Tokeshi et *al*. (1997) for *S. minor*.

In the sandy loam site, trends similar to clay loam related a weed (*A. ambrosiifolia*), $Clay_1$, and MWD to carpogenic germination. The presence of CMQ_1 as biological activity indicator supported the involvement of surface soil biological activity related to higher structural stability (Tokeshi et *al*., 1997). This is the first time these variables are associated with suppression of *S. sclerotiorum* and tested in regression models. Concerning Al concentration (model III, Table 4), to the present knowledge, no suppressive effects of Al were reported against *S. sclerotiorum* or soil-borne disease agent even if its toxicity to plants (Bouton and Parrott, 1997) and soil fauna (Muys et *al*., 2004) is well documented. A suppressiveness of Al concentration could be related to enhanced soil solution concentration as previously reported by Singh et *al*. (1995), but Al was not among the ions involved

in that study. The fact that Al concentration in the soils under study was significantly enhanced by mineral fertilization (Table 1) showed that suppressive processes could be generated by both fertilizations. This might explain why fertilization had no significant effect on carpogenic germination (Chapter 1).

In the clay loam site, the comparison of partial model III controlling for space with model I suggested that most of the sclerotia survival variation was spatially structured and that the correlations with weed biomass (*P. aviculare*), $Sand_1$ and $Clay_2$ were driven by the spatial structure (Table 5) (Fig. 1a-b). Indeed, physical variables were skipped and Total dicotyledons appeared negatively correlated with survival once spatial variation was removed (Table 5). Moreover, as weed cover is conducive for carpogenic germination it is more likely to be suppressive of sclerotia survival as the carpogenic germination induces death of sclerotia (Mitchell and Wheeler, 1990). N content might inhibit sclerotia survival as previously reported (Tenuta and Lazarovits, 2002) where the suppression was attributed to inorganic forms of nitrogen (N), particularly ammonia (NH_4^+; Bailey and Lazarovits, 2003) and nitrous acid (HNO_2) in acidic conditions of sandy soils (Tenuta and Lazarovits, 2002). The suppressive effect of added mineral N on *S. sclerotiorum* was reported by Mitchell and Wheeler (1990), but for carpogenic germination and in controlled conditions only. Therefore, this might be the first time the suppressive effect of N was assessed in field experiment and tested significant using multiple regression analysis.

In the sandy loam site, as the BFI was associated to 3-y-corn rotation in mineral fertilization but with monoculture in urban compost plots, its effect turned secondary when controlling for rotation effect in model II. However, the pH_1 and P_1 remained negatively correlated with sclerotia survival (Table 5). Higher pH was associated with compost (Table 1) and the optimal pH for *S. sclerotiorum* development was reported to be between 4 and 5 (Willetts and Wong, 1980). Even if the compost effect was not significant on sclerotia survival, the mean survival was always lower in compost-amended plots (Chapter 1). The pH of sandy loam was above 7 (Table 1) and consequently greatly above *S. sclerotiorum* optimal, thus compost amendment might have risen pH above an inhibitory threshold. P was already negatively correlated with carpogenic germination in clay loam, but the effect was spatially structured and no causal relationship could be assessed. In this case, sclerotia survival had no significant spatial structure and seems to be inhibited by P_1. Phosphate compounds were already reported to protect plants against fungi but their mode of action was not identified (Barrett et *al*., 2003).

Redundancy analyses

The aerial matrix

In the clay loam site, the partial model II, controlling for rotation or fertilization, appeared very similar to model I and did not affect the chemistry and microbiology variables, contrary to the model III controlling for space (Table 6). In model III, the $PS1_2$ and P_2 were not included and only weed and granulometry variables remained in the model, confirming that no direct causal relationship exists between aerial SSR variables, bacterial counts and phophorus, as previously shown by multiple regression (Tables 3-4). They rather share a common spatial structure. In the model III, as already shown by the regressions (Tables 3-4), the dicotyledon biomass affected apothecia directly and probably DSI indirectly (Fig. 3b). In the regression model on DSI, it was suggested that $Silt_2$ was associated to DSI through a stimulating effect on apothecia development (Table 3). The pRDA model III confirmed this assumption as it showed $Silt_2$ positively correlated to Apothecia but not correlated with DSI (Fig. 3b). According to regression and RDA models, it might be concluded that canopy and soil particle-size were the most important factors that explained the development of the disease, probably by a control of apothecia development and subsequently DSI, the weed canopy being favoured by the interaction Monoculture x Urban Compost.

In the sandy loam site, apothecia were associated with $Clay_1$ which possibly enhanced water potential and then carpogenic germination as previously described (Merriman, 1976; Teo et *al*., 1989) (Tables 4 and 6). In model II (Table 6), SL_2 represented the soil type with finer particle-size in the sandy loam soil (except one plot classified as sandy-clay soil), which supported the importance of a fine soil particle-size to provide minimal conditions for sclerotia germination in sandy loam, particularly in the dry conditions that prevailed during this experiment (cf. regression; Table 4). In model II, apothecia were also negatively correlated with MWD and CMQ_1 (Fig. 4a), as in multiple regression (Table 4), while only CMQ_1 remained in the model III. This sustained that enhanced soil structure and microorganisms act in synergy to suppress the disease, as suggested by Tokeshi et *al*. (1997) to explain suppressive effect induced by inoculation of selected biocontrol organisms or by organic farming practices. Except weed biomass, all the variables retained in the DSI-Apothecia models (Table 6) were associated with Apothecia (Table 4). As DSI and Apothecia were not correlated, the aerial matrix gave little information about the variables driving the disease development, but it showed that the active inoculum (apothecia) was mainly stimulated by weed canopy and inhibited by an higher C mineralization quotient.

The soil matrix

In clay loam model I, most of variables that explained the soil matrix (Table 7) were associated with sclerotia survival (Table 5). Contrary to sandy loam, a higher clay content in fine textured soil induced high water potential that was reported to inhibit carpogenic germination by lack of oxygen and rotting of sclerotia (Teo and Morrall, 1985b). In the presence of compost the soil saturation was probably reduced, which may explain the significant positive effect of compost on sclerotia survival that was noticed in 2001 (Table 2). Although apothecia were strongly correlated with survival (Fig. 5a), the compost was probably also conducive for carpogenic germination as mentionned by Teo and Morrall (1985b) and then, to DSI. The conducive effect of compost on DSI was significant in 2001, as for sclerotia survival (Table 2), but was transient. Indeed, it was no more significant in 2002. More investigation is required to determine if the conducive effect of compost on SSR in clay loam is effectively transient and if suppression may not appear in longer term. Again P_2, that shared a common spatial structure with Apothecia (Table 4), was not retained in model III hence confirming the previous trend noticed in regression. In contrast, the association of N_2 with mineral fertilization in model III (Fig. 5b) was consistent with the suppressive effect of inorganic forms of N on sclerotia survival probably associated with mineral fertilization (Tenuta and Lazarovits, 2002) (Table 2). It was also noticed that the total N was significantly higher in first soil layer in compost amended plots (Table 1), while the survival was affected by total N in the second soil layer in mineral fertilization. This confirmed the qualitative effect of N. However, this suppressive effect of N in 2001 was not persistent as the opposite effect of compost (Table 2). Therefore, it would be worthy to investigate the potential suppressive effect that could originate from compost amendment in a longer term perspective.

In sandy loam model I, contrary to clay loam, higher sclerotia survival was associated with mineral fertilization and monoculture which were both associated with higher biological activity (CMQ_1, BFI_2) (Fig. 6a). The inclusion of Ca in model III refers to multiple regression (Table 5) where survival was negatively correlated with higher pH, generally associated with the presence of Ca in soil. As Ca was significantly enhanced by compost amendment (Table 1), the suppressive effect of compost against sclerotia survival was attributed to the pH enhancement. The pRDA model III clearly illustrated the specific and opposite effect on Apothecia and Survival of the soil variables retained: apothecia were negatively associated with high biological activity and positively with higher Ca concentration as noticed by Singh et *al*. (1995). Survival, however, was positively

correlated with higher biological activity, possibly associated with lower inorganic N concentration (Kuzyakov, 2002; Kuzyakov et *al*., 2000) and was negatively correlated with higher pH indicated by higher Ca concentration.

As expected, the use of multiple regression, RDA and their partial forms, allowed to identify the determinant variables of soil and canopy that influenced the development of SSR of soybean and interacted with the treatments applied. In clay loam, the rotation was found to reduce the disease severity both directly and through the reduction of weed biomass that favoured carpogenic germination. The conducive effect of urban compost was explained by the reduction of water potential at the soil surface, that was found suppressive to carpogenic germination and sclerotia survival in presence of high clay content. In sandy loam, the carpogenic germination was inhibited by biological activity and agregate stability but, correlated positively with Ca, while sclerotia survival reacted to these variables in an opposite way. Such results confirmed the complexity of the interactions that take place in soil ecosystem and that drive the development or suppression of soil-borne diseases as SSR on soybean (Lazarovits, 2001). Globally, the rotation and organic fertilization enhanced soil health as indicated by some determinant physico-chemical variables such as aggregate stability, soil OM content, pH or total C and N concentration. Enhanced soil health was supported by a reduced SSR severity and better soybean yields in the plots with longer rotation or by the interaction of rotation with compost amendment. This trend was not so clear regarding the microbiological indicators, that appeared particularly susceptible to the interaction of rotation with fertilization, along with soil type and probably weather conditions. As a consequence, physico-chemical indicators appeared more suitable to monitor soil health compared with biological indicators, regarding the present knowledge (Rapport et *al*., 1997). However, the statistical tools, developed for numerical ecology such as RDA, allowed to build new hypothesis about the respective roles of soil and canopy variables in the development of the disease. Therefore, multivariate analyses might be determinant for the future development of our soil ecosystem understanding and soil health bioindicators. The models developped here were all significant according to Monte Carlo permutations test and, for the first time provided a strong basis for the future investigation of *S. sclerotiorum* ecology and epidemiology in an global approach including a wide range of ecosystemic variables. Especially, the inclusion of spatial variables in the models allowed to sustain the importance of spatial variability to explain the epidemiology variables, and its importance to detect spurious relationships due to spatial autocorrelation between two or more variables, i. e. two variables may be correlated to a common spatial variation without being related

by a real causal relationship. Spatial autocorrelation is common in nature and is of great concern for the interpretation of ecological experiments (Legendre and Legendre, 1998; Legendre and Trousselier, 1988). The role of spatial structure in explaining SSR variability was further detailed in Chapter 3.

Acknowledgements

The author acknowledges the Conseil des recherches en pêche et en agroalimentaire du Québec (CORPAQ) and the Fédération des producteurs de cultures commerciales du Québec (FPCCQ) financial support for this study. The author gratefully acknowledges Drs. Daniel Borcard and Pierre Legendre for their precious help and skillful assistance in the multivariate analyses. The author is also grateful to Roselyne Labbé for reviewing this chapter.

Table 1: Average values of selected properties of two soils and effects of rotation and fertilization treatments, soil layers and their interactions on physico-chemical and microbiological properties of the two soils from the Saint-Hyacinthe IRDA-CÉROM research station in 1999 and 2002.

	Clay Loam										Sandy Loam									
	1999					2002					1999					2002				
	Mean	Min	Max	Med	Treatment/	Mean	Min	Max	Med	Treatment/	Mean	Min	Max	Med	Treatment/	Mean	Min	Max	Med	Treatment/
Soil variable					Soil layer [y]					Soil layer					Soil layer					Soil layer
Granulometry																				
Clay (%)	34.9	26	51	33	-	-	-	-	-	-	10.0	4.4	18.0	10.5	-	-	-	-	-	-
Silt (%)	21.7	14	28	21	A1	-	-	-	-	-	15.0	9.0	22.1	15.5	-	-	-	-	-	-
Sand (%)	43.5	28	56	44	-	-	-	-	-	-	74.1	68.7	77.6	74.3	-	-	-	-	-	-
Physical																				
MWD [x] (mm)	1.9	0.7	4.1	1.8	-	0.6	0.1	1.8	0.4	UC	0.2	0.1	0.5	0.2	UC	0.1	0.1	0.3	0.1	UC
OM (%)[w]	2.8	2.1	3.8	2.4	UC·A1	3.0	2.0	4.1	2.7	UC·A1	2.7	2.0	3.8	2.8	-	3.1	2.1	4.3	3.0	UC
FC (%)[v]	32.3	27.4	38.1	32.1	UC·A1	34.8	28.9	42.0	35.2	UC	24.3	20.1	30.5	23.9	UC·A1	27.7	22.2	34.0	27.6	UC
Chemical																				
pH	6.7	5.3	7.5	6.2	UC·A1	6.6	5.6	7.4	6.5	UC·A1	7.0	6.3	7.3	6.8	UC·A1	7.1	6.6	7.6	7.1	UC·A1
CEC (meqL-1)[u]	17.9	14.7	21.5	16.9	A1	17.6	13.5	22.8	17.9	NPK	12.7	10.6	16.5	13.5	-	13.8	10.9	17.	13.9	-
total C (%)[t]	1.3	0.8	1.8	1.1	UC·A1	1.4	0.8	2.0	1.2	UC·A1	1.3	0.9	2.0	1.4	-	1.8	1.2	2.5	1.7	UC ; A1
total N (%)	0.13	0.09	0.19	0.12	UC·A1	0.09	0.03	0.15	0.08	UC·A1	0.14	0.10	0.16	0.13	-	0.09	0.06	0.13	0.08	UC ; A1
C/N	9.8	8.0	12.0	9.2	-	15.1	11.7	23.5	13.4	-	9.8	6.9	14.6	10.7	-	20.6	16.8	25.4	20.7	NPK
total S (%)	0.02	0.01	0.05	0.03	NPK; A2	0.04	0.00	0.08	0.05	NPK ; A2	0.01	0.00	0.04	0.02	-	0.03	0.00	0.08	0.04	NPK
P (ppm) [s]	63	19	89	54	A1	55	15	84	54	UC	226	180	315	232	-	231	170	311	234	A2
K (ppm)	242	133	282	195	A1	218	119	296	200	UC·A1	202	80	255	159	-	220	118	302	215	UC ; A1
Ca (ppm)	21000	1308	3033	1677	UC; A1	2034	1383	2846	2017	UC·A1	1780	1267	2338	1838	NPK·A2>UC·A1	2113	1513	2950	2129	UC
Mg (ppm)	338	222	558	279	-	293	184	533	270	-	87	68	119	85	-	92	69	124	88.3	UC
Al (ppm)	912	806	991	884	A1	828	701	968	838	NPK;A2	818	574	1480	922	-	995	654	1390	1030	NPK
Microbiology																				
CMQ [r]	0.12	0.07	0.15	0.12	UC·A2>NPK·A2	0.10	0.06	0.14	0.09	-	0.11	0.06	0.21	0.10	-	0.07	0.04	0.12	0.07	-
PS1 (10^6 cellsmL^{-1})[q]	4.0	0.6	16.2	3.2	-	6.3	0.5	24.0	6.2	-	15.3	5.4	45.6	10.5	R1>R3	33.2	2.5	68.3	41.9	R1·NPK>R2·NPK
PS2 (10^6 cellsmL^{-1})[q]	5.9	1.3	19.3	3.3	-	6.3	0.1	25.8	2.8	A1	13.7	4.3	44.0	9.0	-	45.3	2.9	89.5	48.5	R3·UC>R1·UC
BFI	0.07	0.00	0.46	0.04	-	0.04	0.00	0.43	0.00	-	0.16	0.00	1.21	0.02	-	0.04	0.00	0.72	0.00	R3·NPK>R1·NPK

[y] The columns (Treatment/Soil layers) show treatments (rotation and fertilization), soil layers and their interactions (·)which have a significant positive effect on soil variables (qualitative contrasts, $P < 0.05$); treatments for rotation are: R1 (3-y-corn rotation), R2 (2-y-corn rotation), R3 (soybean monoculture); treatments for fertilization are : mineral fertilization (NPK), and Urban Compost (UC); soil layers are A1 (0-10 cm) and A2 (10-20 cm); ">" indicates a higher mean value for the treatment or interaction considered.

[x] MWD : Mean Weight Diameter = ∑ (mean diameter x aggregates weight)/sample dry weight (Kemper and Rosenau, 1986)

[w] OM : Organic Matter (%) = (weight at 105°C-weight at 420°C)/(weight of air dried soil) * 100 (CPVQ, 1988)

[v] FC : Field Capacity (Cassel and Nielsen, 1986)

[u] CEC : Cation Exchange Capacity was calculated : CEC(meq/100) = [(7.5 - pH buffer) * 9] + [K] + [Ca] + [Mg] (AFEQ, 1990)

[t] C, N, S concentrations determined by LECO CNS 2000 ®

[s] P, K, Ca, Mg, Al determined by Mehlich III extraction method

[r] CMQ : C Mineralization Quotient, in 10-20 cm soil depth, after 41d soil incubation at 28°C, CMQ = (mg C/ mg C total) * 100 (Dommergues, 1960)

[q] Bacterial cells direct counts with Neubauer haemocytometer of soil (10-20 cm) suspension filtrate after 48h incubation at 28°C, in a physiologic saline solution (PS1) or, in a physiologic saline solution plus 5 gL^{-1} Lactose and 5 gL^{-1} Dextrose (PS2) (Rusch, 1972)

[p] BFI : Biological Fertility Index (Rusch, 1972)

Table 2: Effects of rotation and fertilization treatments and their interactions on SSR disease variables and plant canopy (LAI, weed biomass and yields of soybean) variables in two soils from the Saint-Hyacinthe IRDA-CÉROM research station, in 2001 and 2002.

	Clay Loam										Sandy Loam									
SSR disease and	**2001**					**2002**					**2001**					**2002**				
canopy variables	**Mean**	**Min**	**Max**	**Med**	**Treatment[z]**	**Mean**	**Min**	**Max**	**Med**	**Treatment**	**Mean**	**Min**	**Max**	**Med**	**Treatment**	**Mean**	**Min**	**Max**	**Med**	**Treatment**
***Sclerotinia* stem rot**																				
DSI (%)[y]	5.9	2.0	14.3	5.7	UC	24.0	0.0	88.7	12.3	R2 ; R3	11.8	4.0	21.3	11.8	All>R3·NPK	59.9	20.0	96.0	61.3	All>R1·UC
Apothecia (# m^{-2})	0.2	0.0	0.7	0.0	-	0.1	0.0	1.1	0.0	-	0.8	0.0	6.7	0.5	-	0.2	0.0	0.8	0.1	NS
Sclerotia survival (%)	20.7	1.5	71.2	23.3	UC	13.8	0.5	47.8	9.1	-	23.4	0.5	65.9	36.4	-	13.8	0.0	37.3	14.3	NS
Soybean Leaf Area Index[x]																				
Stage R2-R3[w]	2.8	2.0	4.9	2.6	-	0.4	0.1	1.1	0.4	R1·UC	3.8	2.2	4.4	4.1	-	0.5	0.1	1.2	0.4	NS
Stage R5-R6[w]	5.1	2.6	6.3	5.5	-	0.4	0.1	1.4	0.3	-	4.7	4.2	6.3	4.5	R3·UC	0.4	0.0	1.6	0.2	NS
Yields (Kg soybean Ha^{-1})	2150	1065	2747	2298	R2	862	165	2296	666	R1·UC	1792	854	2557	1787	-	341	37	1384	170	R1
Weed biomass (KgHa^{-1})																				
Amaranthus retroflexus	210	-	1373	-	NPK	204	-	860	70	-	290	-	1567	123.3	-	486	-	2580	243	NS
Chenopodium album	788	-	3033	420	NPK	526	-	2440	410	-	2157	-	6000	1910	R2·NPK	5211	153	16847	3773	R2>R3
Ambrosia artemisiifolia	5223	-	32746	2423	R3·UC	14682	47	41553	13147	R3 ; UC	4661	20	22546	2600	R3·UC	12934	73	39026	11840	R3>R1
Brassica kaber	380	-	2280	90	R1	2223	-	11193	1547	R1>R3	92	-	893	-	-	1158	-	5300	507	NS
Polygonum aviculare	103	-	1753	-	-	34	0	333	-	-	112	-	2173	-	-	67	-	1060	-	NS
Dicotyledon	7037	440	33386	4487	R3·UC	18025	3780	43220	15627	R3·UC	7314	1400	26413	6530	R3·UC	20021	7407	42520	19150	NS
Monocotyledon	1913	-	20860	720	-	9303	1820	20733	8337	NPK	3042	-	13633	1853	R3>R1	14470	2107	29513	13830	R3·NPK>R1·NPK
Total biomass	8951	600	33526	5753	R3·UC	27371	5600	55073	26506	R3·UC>R1·UC	10356	2187	30820	6997	R3·UC>R1·UC	34491	18133	63879	33196	R3

[z] The columns (Treatment) show treatments (rotation and fertilization) and their interactions (·) which have a significant positive effect on SSR disease and plant canopy variables (qualitative contrasts, $P < 0.05$); treatments for rotation are: R1 (3-y-corn rotation), R2 (2-y-corn rotation), R3 (soybean monoculture); treatments for fertilization are : mineral fertilization (NPK), and Urban Compost (UC); ">" indicates a higher mean value for the treatment or interaction considered.

[y] DSI : Disease Severity Index (Grau and Radke, 1984)

[x] Leaf area index (LAI ; leaf area per unit of ground area) was measured with a Plant Canopy Analyser LAI-2000 by LI-Cor ®

[w] Soybean stages R2-R3: full bloom- beginning pod; R5-R6: beginning seed- full seed (Fehr et *al*., 1971)

Table 3: Disease severity (DSI) variance explained by environmental variables retained after forward selection in the multiple regression based on all sets of environmental variables (additive selection) in the clay loam and sandy loam sites in 2002.

	Clay loam								Sandy loam											
	Model I				Model II Rotation				Model I				Model II Rotation x Fertilization				Model III x, xy^2, x^2y^3			
Covariable																				
Variable set	*Variable*	R^2	r	P-value	*Variable*	R^2	r	P-value	*Variable*	R^2	r	P-value	*Variable*	R^2	r	P-value	*Variable*	R^2	r	P-value
Canopy	***Yield***	51	-0.71	0.001					***Tweeds***	24	-0.49	0.013	***Tweeds***	30	0.59	0.004				
	LAI1	10	0.01	0.025					***Ama. ret.***	10	-0.28	0.075								
Physics	***$Silt_2$***	6	-0.35	0.089	***$Silt_2$***	20	0.35	0.012	***OM_2***	11	0.46	0.057								
Chemistry	***S_2***	8	0.43	0.017	***S_2***	14	-0.56	0.005					***C_1***	8	-0.46	0.068	***P_2***	9	0.43	0.056
																	CEC_2	10	-0.05	0.025
Microbiology	***$PS1_2$***	6	0.19	0.044																
Overall model		80.5	0.9	0.001		34.2	0.73	0.002		45.2	0.67	0.008		38.3	0.67	0.004		19.1	0.63	0.017

x, xy^2, x^2y^3: terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)
LAI_1: Leaf area index (LAI ; leaf area per unit of ground area) was measured with a Plant Canopy Analyser LAI-2000 by LI-Cor ®
$Silt_2$: Silt content (%) in 10-20 cm soil layer (A_2)
S_2: Sulphur in A_2 soil layer
$PS1_2$: Bacterial cells direct counts with Neubauer haemocytometer of soil (10-20 cm) suspension filtrate after 48h incubation at 28°C, in a physiologic saline solution
OM_2: Organic Matter (%) in A_2 = (weight at 105°C-weight at 420°C)/(weight of air dried soil) * 100 (CPVQ, 1988)
Ama. ret.: *Amaranthus retroflexus* aerial biomass ($KgHa^{-1}$)
Tweeds: Total aerial weed biomass ($KgHa^{-1}$)
C_1: Carbon concentration in 0-10 cm soil layer (A_1) determined by LECO CNS 2000 ®
CEC_2: Cation Exchange Capacity in A_2 was calculated : CEC(meq/100) = [(7.5 - pH buffer) * 9] + [K] + [Ca] + [Mg] (AFEQ, 1990).

Table 4 : Carpogenic germination (Apothecia) variance explained by environmental variables retained after forward selection in the multiple regression based on all sets of environmental variables (additive selection), in the clay loam and sandy loam sites in 2002.

	Clay loam								Sandy loam							
	Model I				Model III				Model I				Model III			
Covariable					xy, x^2y^2, x^2y^3								y^3			
Variable set	*Variable*	R^2	r	P value	*Variable*	R^2	r	P value	*Variable*	R^2	r	P value	*Variable*	R^2	r	P value
Canopy	***Tdicot.***	20	0.61	0.006	***Tdicot.***	4	0.5	0.039	*Amb. art.*	9	0.57	0.039	*Amb. art.*	13	0.42	0.048
Physics	***CS_2***	13	0.29	0.007	***CS_2***	3	0.3	0.032	***$Clay_1$***	35	0.59	0.005	***MWD***	9	-0.25	0.041
					MWD	2	-0.18	0.035	***MWD***	18	-0.23	0.013	***$Clay_1$***	8	0.41	0.048
Chemistry	***P_2***	37	-0.61	0.007									***Al_1***	4	-0.25	0.083
	Al_2	10	-0.04	0.008									***Al_2***	6	-0.12	0.029
Microbiology	***$PS1_1$***	3	0.47	0.096					***CMQ_1***	8	-0.33	0.034	***CMQ_1***	15	-0.29	0.023
Overall model		82.9	0.91	0.001		8.9	0.75	0.001		70.4	0.84	0.001		55.1	0.86	0.002

xy, x^2y^2, x^2y^3,y^3: terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)
Tdicot: Total aerial dicotyledons biomass ($KgHa^{-1}$)
Amb. art.: *Ambrosia artemisiifolia* aerial biomass ($KgHa^{-1}$)
CS_2: Clay soil in 10-20 cm (A_2)
$Clay_1$: Clay content (%) in 0-10 cm soil layer (A_1)
MWD: Mean Weight Diameter = $\sum$ (mean diameter x aggregates weight)/sample dry weight (Kemper and Rosenau, 1986)
P_2: Phosphorus concentration (ppm) in A_2
Al_1 : Aluminium concentration (ppm) in A_1
Al_2 : Aluminium concentration (ppm) in A_2
$PS1_1$: Bacterial cells direct counts with Neubauer haemocytometer of soil (0-10 cm) suspension filtrate after 48h incubation at 28°C, in a physiologic saline solution
CMQ_1: C Mineralization Quotient, in 0-10 cm soil depth, after 41d soil incubation at 28°C, CMQ = (mg C/ mg C total) * 100 (Dommergues, 1960).

Table 5: Sclerotia survival (Survival) variance explained by environmental variables retained after forward selection in the multiple regression based on all sets of environmental variables (additive selection), in the clay loam and sandy loam sites in 2002.

	Clay loam								Sandy loam							
	Model I				Model III x^3y, x^2y^2, x^2y^3				Model I				Model II Rotation			
Covariable																
Variable set	***Variable***	**R^2**	**r**	**P value**	***Variable***	**R^2**	**r**	**P value**	***Variable***	**R^2**	**r**	**P value**	***Variable***	**R^2**	**r**	**P value**
Canopy	***Pol. avi.***	11	0.43	0.029	***Tdicot.***	4	-0.3	0.052								
Physics	***$Sand_1$***	11	0.36	0.026												
	$Clay_2$	17	0.07	0.005												
Chemistry	***N_2***	40	-0.63	0.002	***N_2***	7	-0.51	0.008	***P_1***	17	-0.37	0.028	***pH_1***	22	-0.5	0.017
									pH_1	14	-0.44	0.018	***P_1***	10	-0.33	0.073
Microbiology									***BFI_1***	20	0.45	0.017	***BFI_1***	11	0.41	0.017
Overal model		78.5	0.89	0.001		11	0.64	0.015		51.5	0.72	0.003		43.4	0.71	0.004

x^3y, x^2y^2, x^2y^3 : terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)
Pol. avi.: Polygonum aviculare aerial biomass ($KgHa^{-1}$)
Tdicot.: Total aerial dicotyledons biomass ($KgHa^{-1}$)
$Sand_1$: Sand content (%) in 0-10cm (A_1)
$Clay_2$: Clay content (%) in 10-20 cm soil layer (A_2)
N_2: Nitrogen concentration (%) in A_2
P_1: Phosphorus concentration (ppm) in A_1
pH_1: pH in A_1
BFI_1: Biological Fertility Index in A_1 (Rusch, 1972).

Table 6: Disease severity (DSI) and carpogenic germination (Apothecia) (aerial matrix) variance explained by environmental variables retained after forward selection in the RDA based on all sets of environmental variables (additive selection), in the clay loam and sandy loam sites in 2002.

	Clay loam									Sandy loam								
	Model I			Model II			Model III			Model I			Model II			Model III		
Covariable				Rotation (Fertilization)			xy, x^3y, x^2y^2, x^2y^3						Rotation x Fertilization			y^3		
Variable set	*Variable*	R^2	P-value	*Variable*	R^2	P-value	*Variable*	R^2	P-value	*Variable*	R^2	P-value	*Variable*	R^2	P-value	*Variable*	R^2	P-value
Canopy	***Tdicot***	41	0.001	***Tdicot.***	26 (33)	0.003 (0.001)	***Tdicot.***	18	0.003	*Amb. art.*	24	0.005	*Amb. art.*	25	0.004	*Amb. art.*	12	0.031
	Pol. avi.	6	0.057	***Pol. avi.***	7 (9)	0.026 (0.007)												
Physics							***$Silt_2$***	4	0.073	***SL_2***	8	0.065	***SL_2***	7	0.09			
										MWD	8	0.033						
Chemistry	***P_2***	13	0.003	***P_2***	10 (13)	0.012 (0.003)				***$Clay_1$***	6	0.079						
Microbiology	***$PS1_1$***	5	0.075	***$PS1_1$***	6 (5)	0.055 (0.09)				***CMQ_1***	13	0.023	***CMQ_1***	12	0.015	***CMQ_1***	10	0.057
Overall model		65.4	0.001		48.6 (59.7)	0.001		21.5	0.001		59.2	0.001		43.7	0.002		21.8	0.011

$xy, x^3y, x^2y^2, x^2y^3, y^3$: terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)
Tdicot.: Total aerial dicotyledons biomass ($KgHa^{-1}$)
Amb. art.: *Ambrosia artemisiifolia* aerial biomass ($KgHa^{-1}$)
Pol. avi.: *Polygonum aviculare* aerial biomass ($KgHa^{-1}$)
$Silt_2$: Silt content (%) in 10-20 cm soil layer (A_2)
SL_2: Sandy loam soil in A_2
MWD : Mean Weight Diameter = ∑ (mean diameter x aggregates weight)/sample dry weight (Kemper and Rosenau, 1986)
P_2: Phosphorus concentration (ppm) in A_2
$Clay_1$: Clay content (%) in 0-10 cm soil layer (A_1)
$PS1_1$: Bacterial cells direct counts with Neubauer haemocytometer of soil (0-10 cm) suspension filtrate after 48h incubation at 28°C, in a physiologic saline solution
CMQ_1: C Mineralization Quotient, in A_1, after 41d soil incubation at 28°C, CMQ = (mg C / mg C total) * 100 (Dommergues, 1960).

Table 7: Carpogenic germination (Apothecia) and sclerotia survival (Survival) (soil matrix) variance explained by environmental variables retained after forward selection in the RDA based on all sets of environmental variables (additive selection), in the clay loam and sandy loam sites in 2002.

	Clay loam						Sandy loam					
	Model I			Model III			Model I			Model III		
Covariable				x^3y, x^2y^2, x^2y^3						y^3		
Variable set	*Variable*	R^2	P-value	*Variable*	R^2	P-value	*Variable*	R^2	P-value	*Variable*	R^2	P-value
Canopy	***Tdicot.***	6	0.037	***Tdicot.***	4	0.017	*Amb. art.*	24	0.002	*Amb. art.*	16	0.009
	Pol. avi.	5	0.057									
Physics	***CL_2***	21	0.001									
	$Clay_1$	5	0.102									
Chemistry	***P_2***	35	0.003	***N_2***	4	0.026				***Ca_1***	14	0.014
Microbiology							***CMQ_1***	16	0.012	***CMQ_1***	8	0.053
							BFI_2	9	0.036			
Overall model		71.8	0.001		7.6	0.008		49.1	0.001		38.3	0.001

x^3y, x^2y^2, x^2y^3, y^3: terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)
Tdicot. : Total aerial dicotyledons biomass ($KgHa^{-1}$)
Amb. art.: *Ambrosia artemisiifolia* aerial biomass ($KgHa^{-1}$)
Pol. avi.: *Polygonum aviculare* aerial biomass ($KgHa^{-1}$)
CL_2: Clay loam soil in 10-20 cm soil layer (A_2)
$Clay_1$: Clay content (%) in 0-10 cm soil layer (A_1)
P_2: Phosphorus concentration (ppm) in A_2
N_2: Nitrogen concentration (%) in A_2
Ca_1: Calcium concentration (ppm) in A_1
CMQ_1: C Mineralization Quotient, in A_1, after 41d soil incubation at 28°C, CMQ = (mg C / mg C total) * 100 (Dommergues, 1960)
BFI_2: Biological Fertility Index in A_2 (Rusch, 1972).

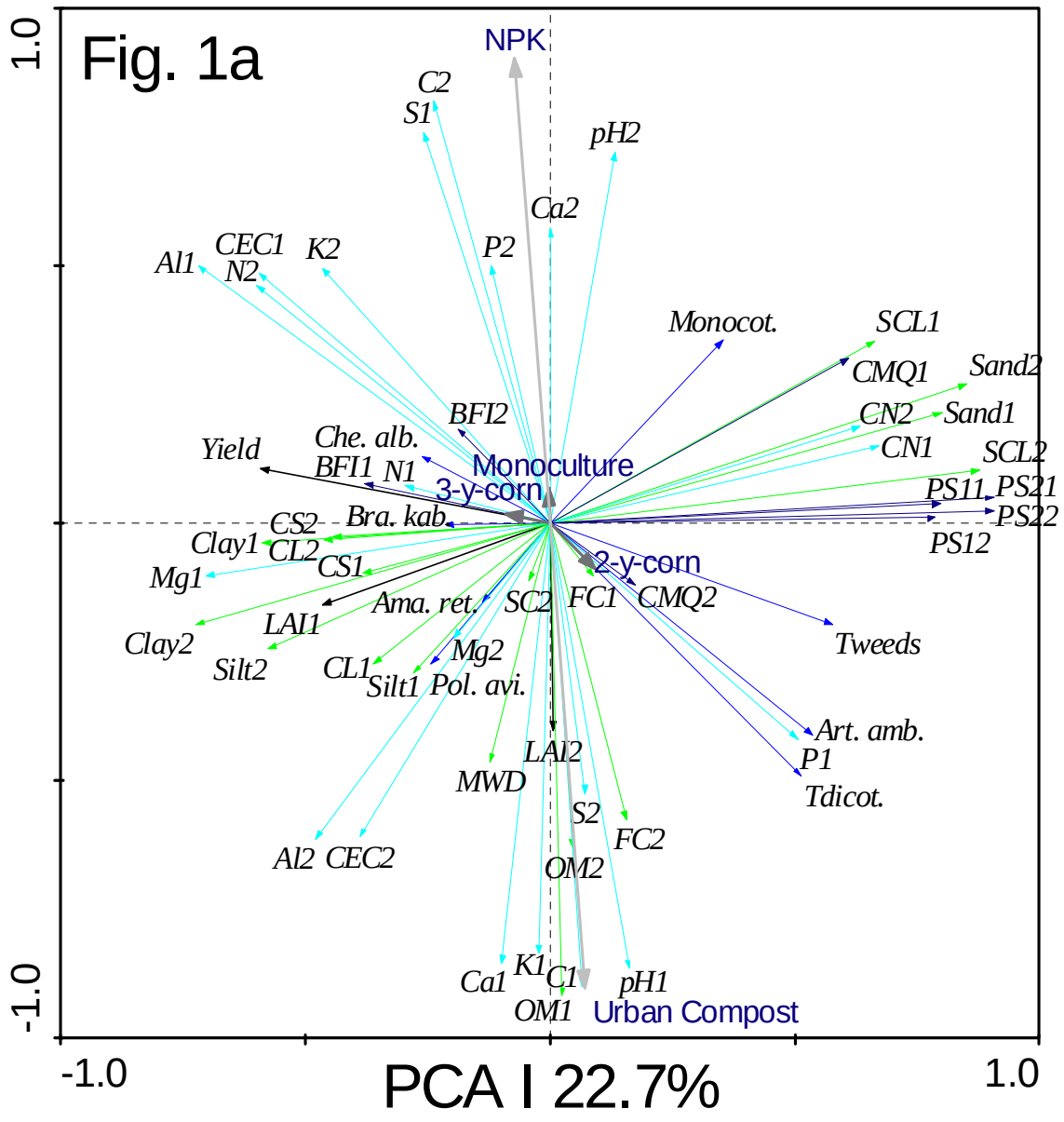
Fig. 1a
NPK
C2
S1
pH2
Ca2
P2
Al1
CEC1
N2
K2
Monocot.
SCL1
CMQ1
Sand2
CN2
Sand1
CN1
SCL2
PS11
PS21
PS22
PS12
BFI2
Che. alb.
Yield
BFI1
N1
Monoculture
3-y-corn
Bra. kab.
CS2
Clay1
CL2
CS1
Mg1
2-y-corn
Ama. ret.
SC2
FC1
CMQ2
LAI1
Clay2
Silt2
CL1
Mg2
Silt1
Pol. avi.
Tweeds
Art. amb.
P1
Tdicot.
LAI2
MWD
S2
FC2
Al2
CEC2
OM2
Ca1
K1
C1
pH1
OM1
Urban Compost
1.0
-1.0
-1.0
1.0
PCA I 22.7%
PCA II 17.6%

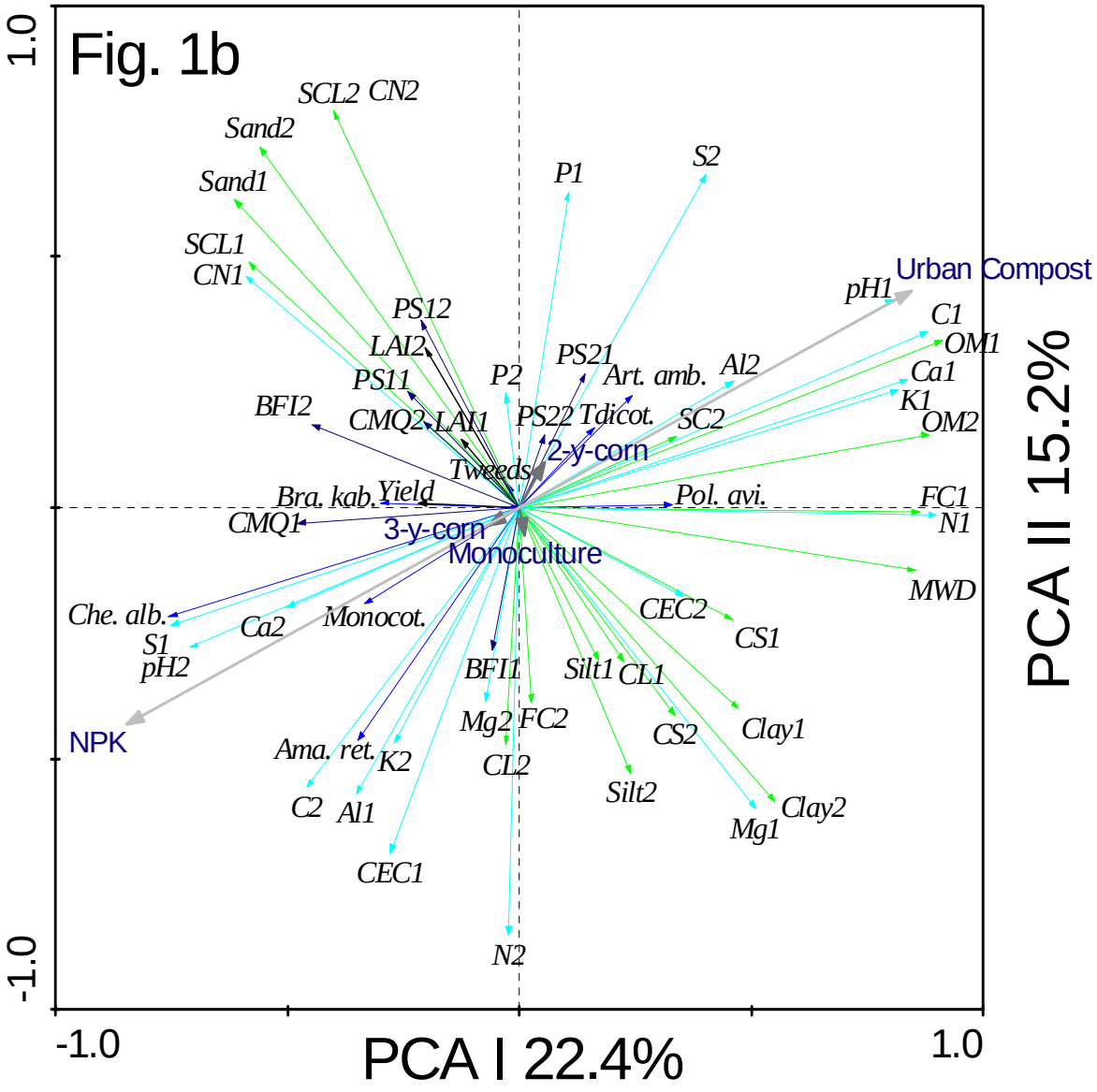

Figure 1: Clay loam 2002 (a) and 2001 (b) PCA biplots of correlations between all soil and canopy variables plus treatments (rotation and fertilization) as complementary variables. Variables are labeled $_1$ when estimated in A_1 (0-10 cm), and labeled $_2$ when estimated in A_2 (10-20 cm). 3-y-corn rotation; 2-y-corn rotation; monoculture: soybean monoculture; NPK: mineral fertilization treatment; Urban Compost: urban compost treatment; Al: aluminium concentration; BFI: biological fertility index; C: carbon concentration; Ca: calcium concentration; CEC: cation exchange capacity; CL: clay loam ; Clay: clay content; CMQ: carbon mineralization quotient; CN: carbon to nitrogen ratio; CS: clay soil; DSI: disease severity index; K: potassium concentration; LAI: leaf area index; Mg: magnesium concentration; MWD: mean weight diameter; N: nitrogen concentration; OM: organic matter content; P: phosphorus concentration; PS1: bacterial cells direct counts in physiologic saline solution; PS2: bacterial cells direct counts in physiologic saline solution plus 5 gL^{-1} lactose and 5 gL^{-1} dextrose; S: sulfur concentration; Sand: sand content; SCL: sand-clay loam; SL: sandy loam; Silt: silt content; *Amb. art.*: *Ambrosia artemisiifolia* biomass; *Ama. ret.*: *Amaranthus retroflexus* biomass; *Bra. kab.: Brassica kaber* biomass; *Che. alb.: Chenopodium* album biomass; Monocot: total monocotyledons biomass; *Pol. avi.: Polygonum aviculare* biomass; Tdicot.: total dicotyledons biomass; Tweeds: total weed biomass.

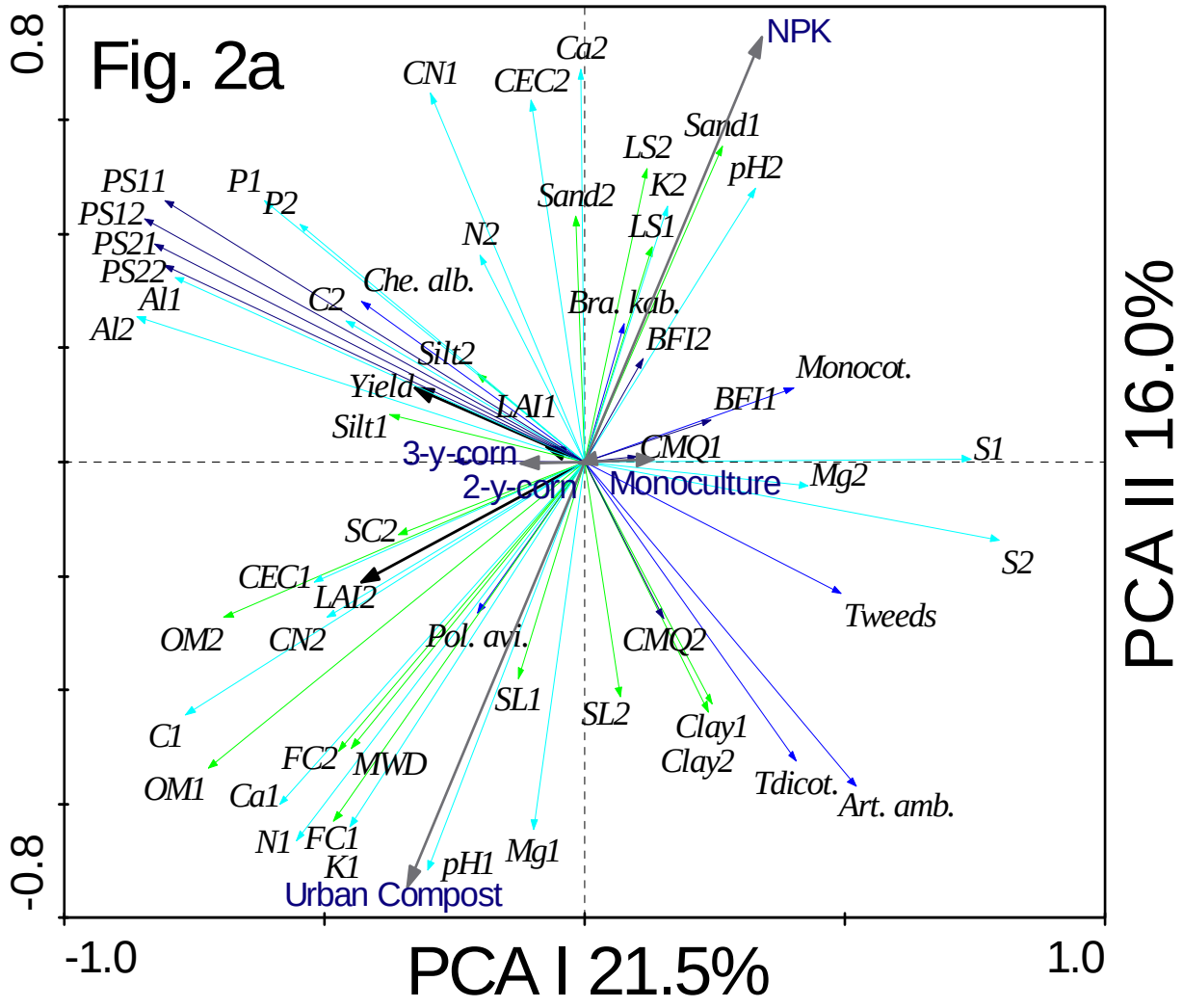
Fig. 2a
NPK
Ca2
CN1
CEC2
Sand1
LS2
pH2
K2
PS11
P1
P2
Sand2
PS12
LS1
N2
PS21
PS22
Che. alb.
C2
Bra. kab.
Al1
Al2
BFI2
Silt2
Monocot.
Yield
BFI1
LAI1
Silt1
CMQ1
S1
3-y-corn
Mg2
2-y-corn
Monoculture
SC2
S2
CEC1
LAI2
Tweeds
OM2
CN2
Pol. avi.
CMQ2
SL1
SL2
C1
Clay1
FC2
MWD
Clay2
OM1
Ca1
Tdicot.
Art. amb.
N1
FC1
K1
pH1
Mg1
Urban Compost
0.8
-0.8
-1.0
1.0
PCA I 21.5%
PCA II 16.0%

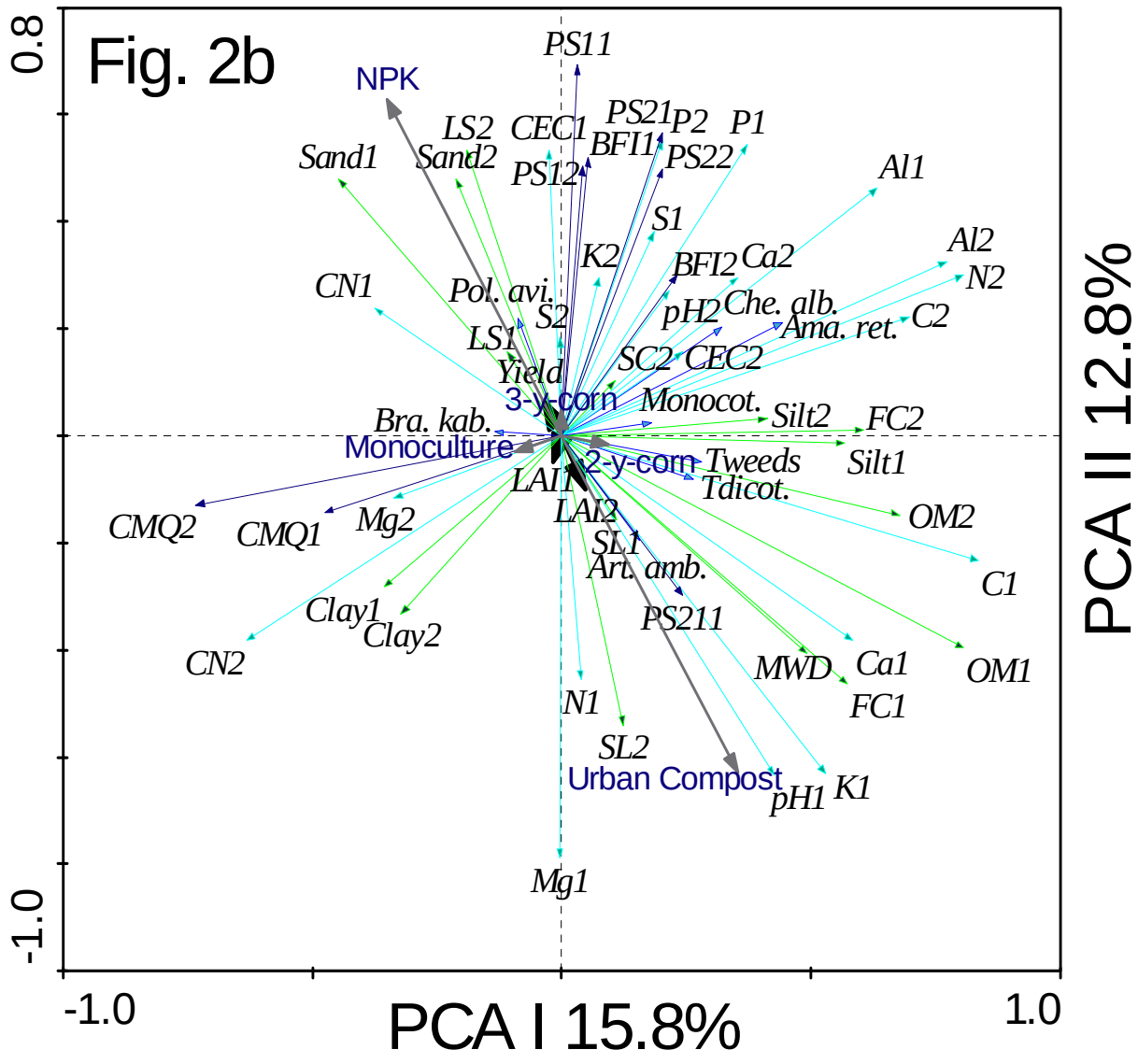

Figure 2: Sandy loam 2002 (a) and 2001 (b) PCA biplots of correlations between all soil and canopy variables plus treatments (rotation and fertilization) as complementary variables. Abbreviations of variables and treatments are given in Fig. 1.

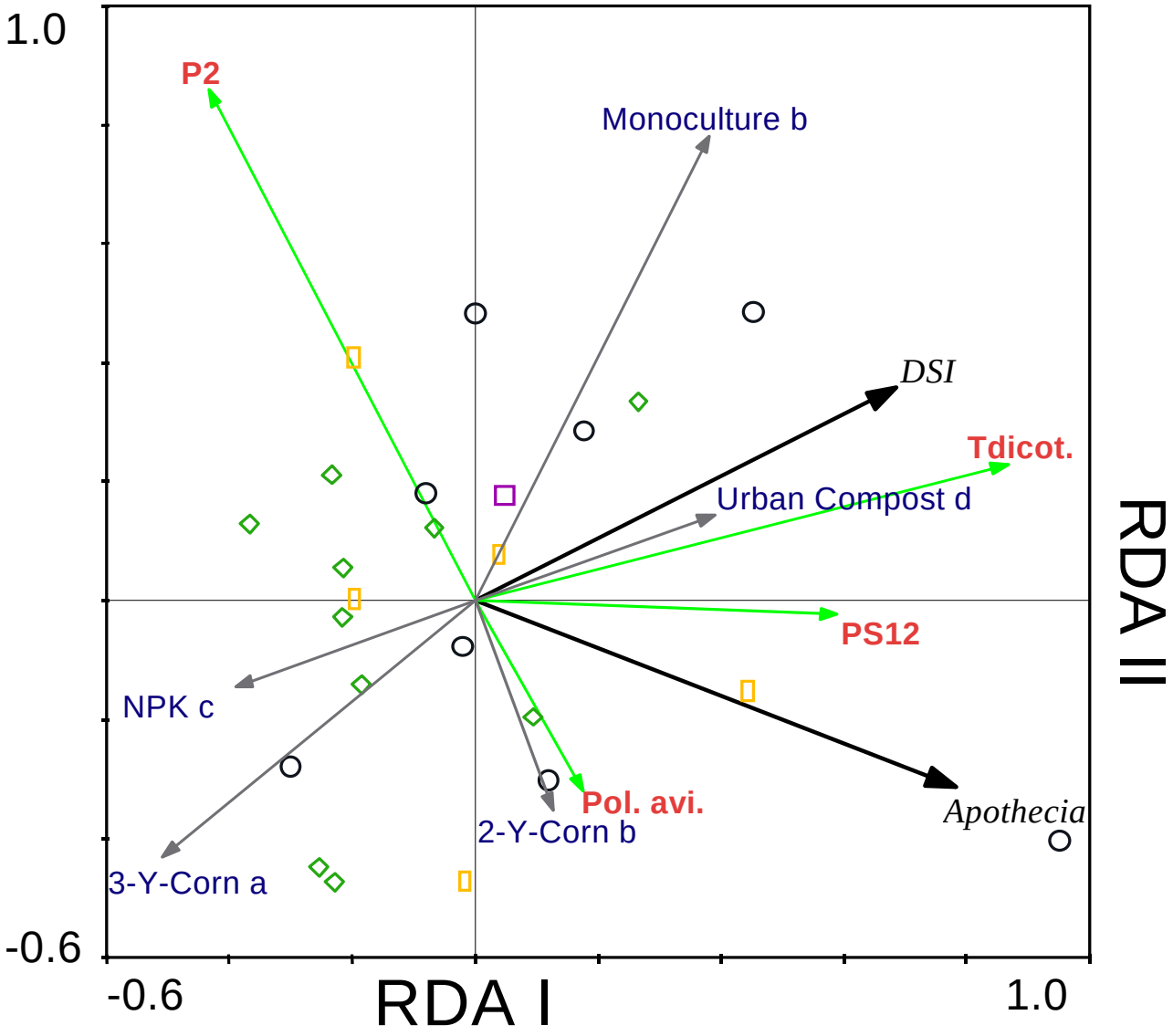

Figure 3a. Clay loam, 2002: redundancy analysis (RDA) correlation triplot of disease severity (*DSI*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by additive forward selection (model I, $P = 0.001$). Abbreviations of variables and treatments are given in Fig. 1. The treatments rotation and fertilization are included as passive variables in the analysis. Same letters indicate no significant differences ($P < 0.05$) according to MANOVA-like analysis (split-plot option, CANOCO 4.5). Samples are classified by soil type: ○ Sand-clay loam; ▯ Sand-clay soil; ◊ Clay loam; □ Clay soil. The RDA axis I displays 54.1% and axis II 13.3% of the DSI-Apothecia matrix.

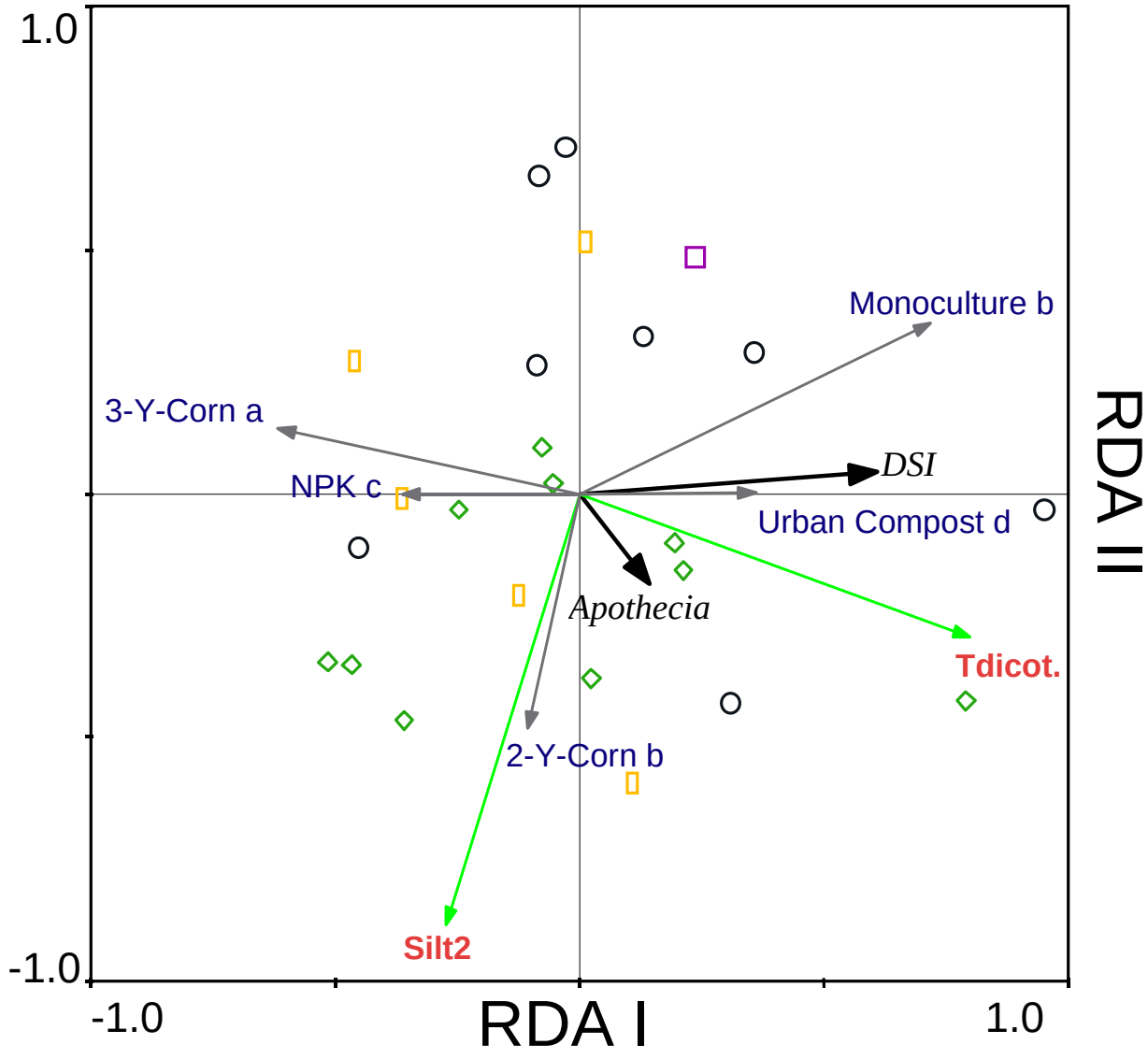

Figure 3b. Clay loam, 2002: partial redundancy analysis (pRDA) correlation triplot of disease severity (*DSI*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by additive forward selection controlling for space (model III, $P = 0.001$). Abbreviations of variables and treatments are given in Fig. 1. The treatments rotation and fertilization are included as passive variables in the analysis. Same letters indicate no significant differences ($P < 0.05$) according to MANOVA-like analysis (split-plot option, CANOCO 4.5). Samples are classified by soil type: ○ Sand-clay loam; ▯ Sand-clay soil; ◊ Clay loam; □ Clay soil. The RDA axis I displays 19.7% and axis II 1.8% of the DSI-Apothecia matrix.

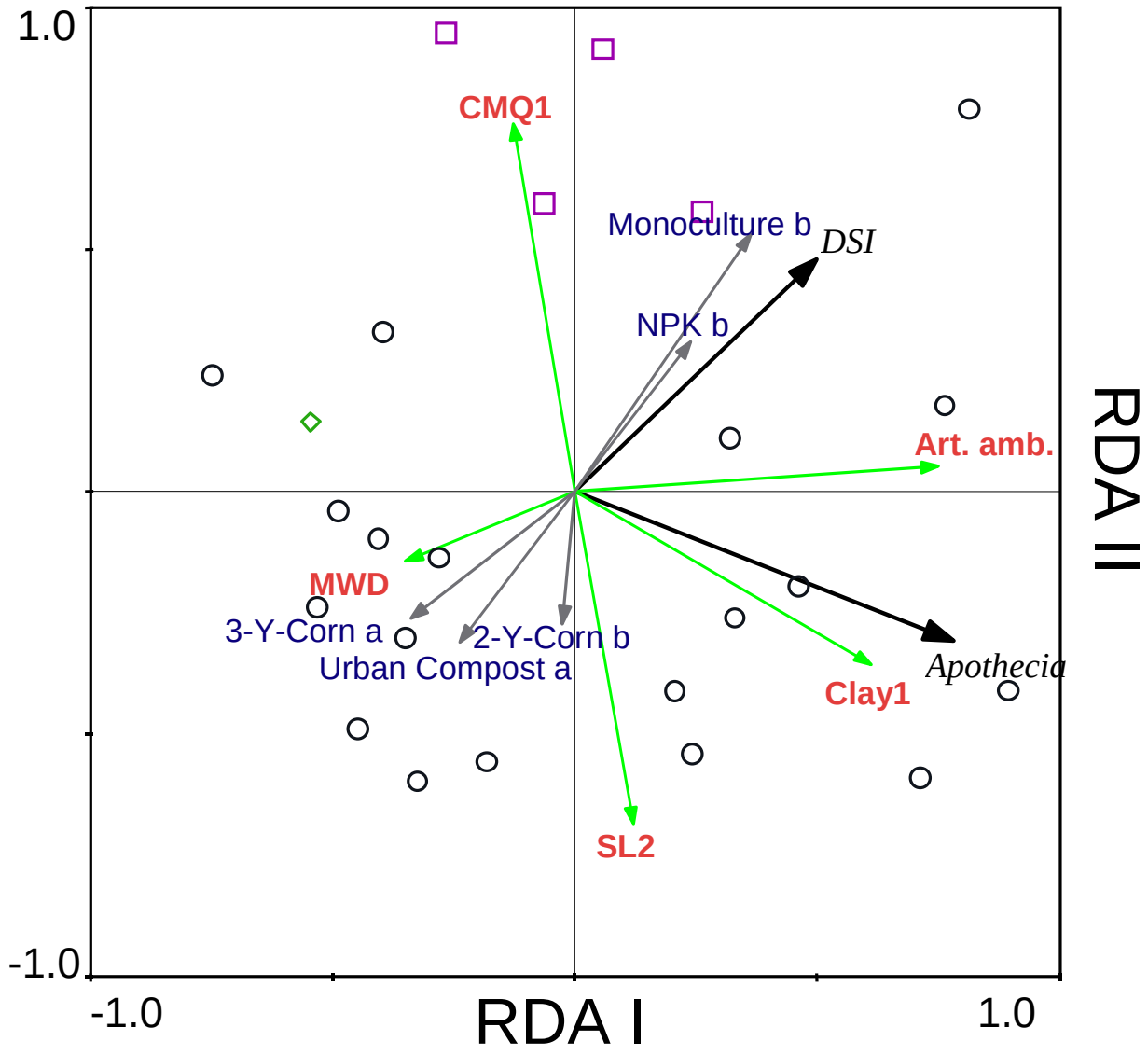

Figure 4a. Sandy loam, 2002: redundancy analysis (RDA) correlation triplot of disease severity (*DSI*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by additive forward selection (model I, $P = 0.001$). Abbreviations of variables and treatments are given in Fig. 1. The treatments rotation and fertilization are included as passive variables in the analysis. Same letters indicate no significant differences ($P < 0.05$) following MANOVA-like analysis (split-plot option, CANOCO 4.5). Samples are classified by soil type: ○ Sandy loam; □ Loamy sand; ◊ Sand-clay soil. The RDA axis I displays 43.0% and axis II 16.3% of the DSI-Apothecia matrix.

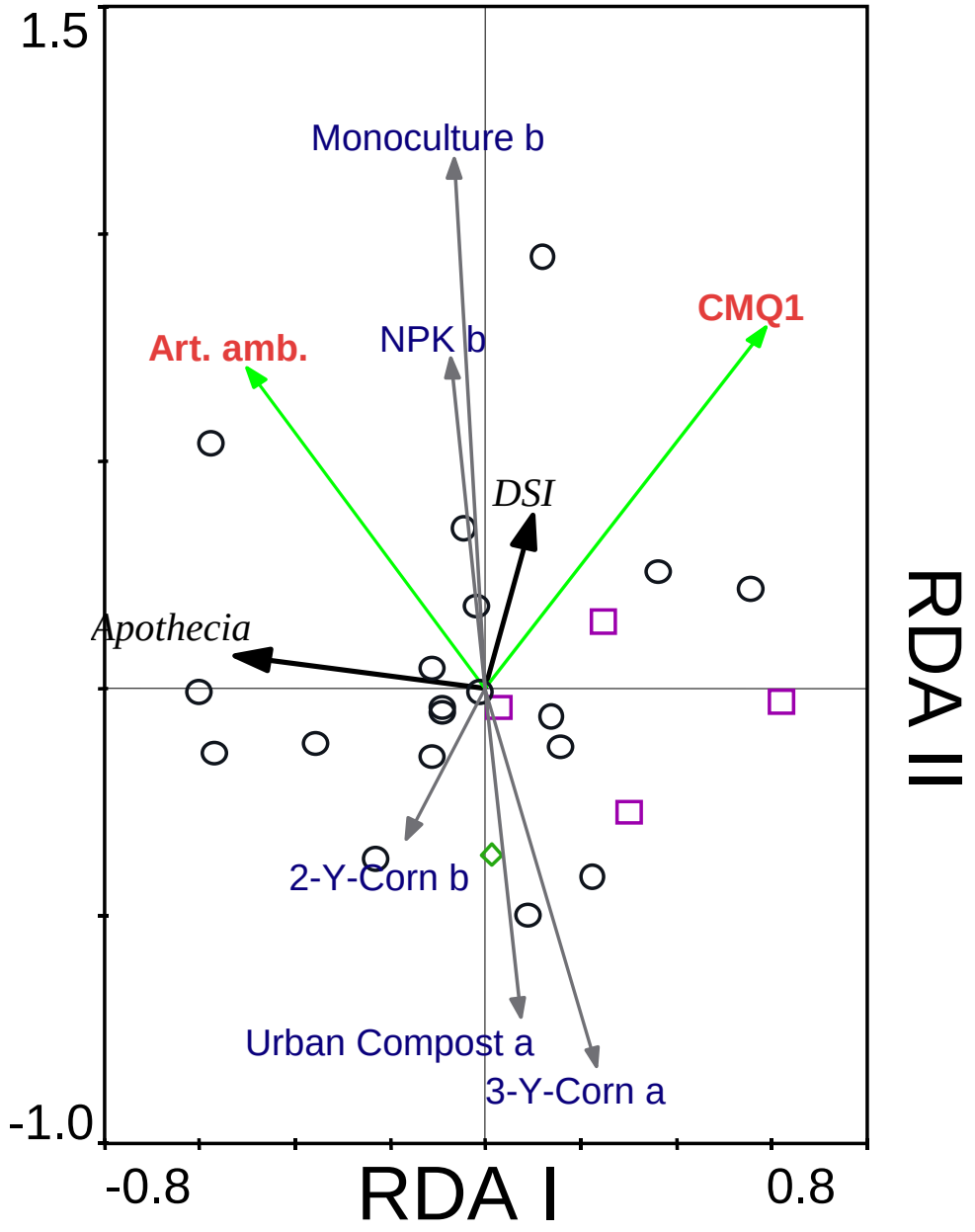

Figure 4b. Sandy loam, 2002: partial redundancy analysis (pRDA) correlation triplot of disease severity (*DSI*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by additive forward selection controlling for space (model III, $P = 0.011$). Abbreviations of variables and treatments are given in Fig. 1. The treatments rotation and fertilization are included as passive variables in the analysis. Same letters indicate no significant differences ($P < 0.05$) following MANOVA-like analysis (split-plot option, CANOCO 4.5). Samples are classified by soil type: ○ Sandy loam; □ Loamy sand; ◊ Sand-clay soil. The RDA axis I displays 14.3% and axis II 7.5% of the DSI-Apothecia matrix.

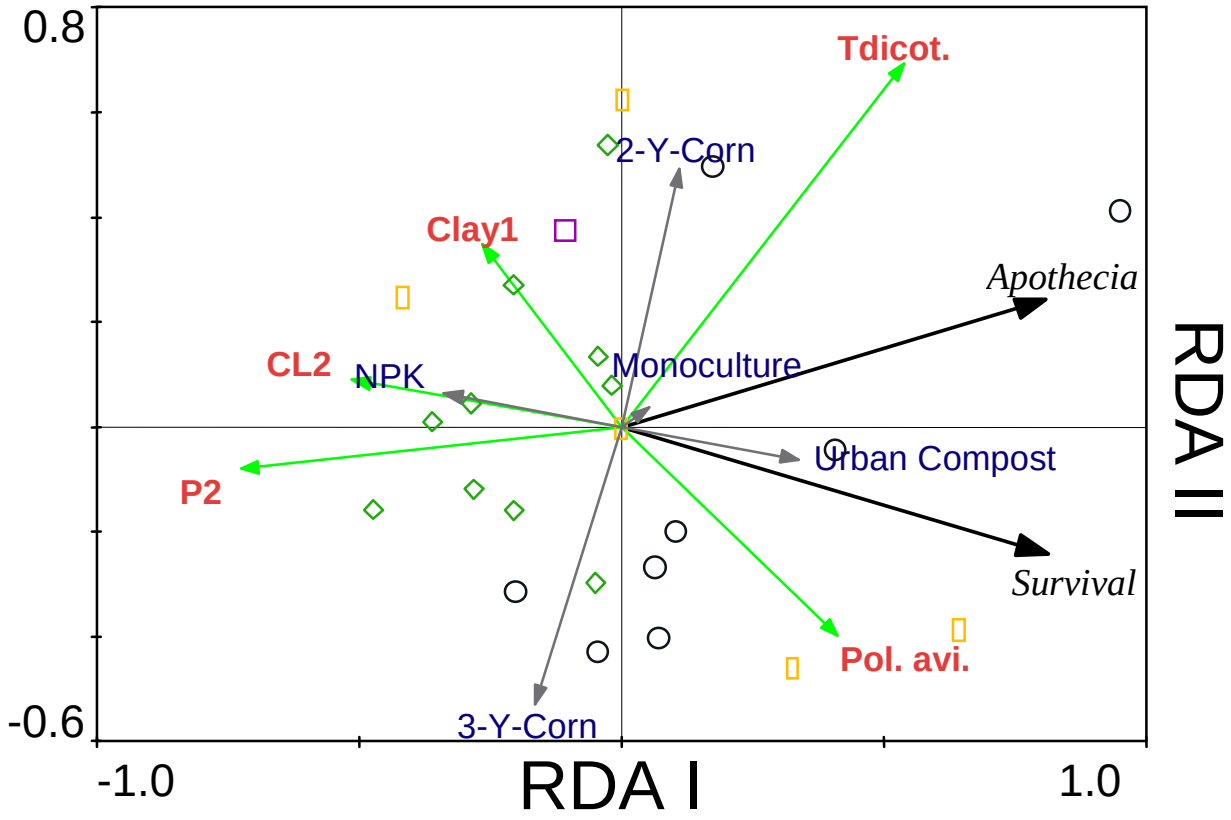

Figure 5a. Clay loam, 2002: redundancy analysis (RDA) correlation triplot of sclerotia survival (*Survival*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by additive forward selection (model I, P = 0.001). Abbreviations of variables and treatments are given in Fig. 1. The treatments rotation and fertilization are included as passive variables in the analysis. Samples are classified by soil type: ○ Sand-clay loam; ▯ Sand-clay soil; ◊ Clay loam; □ Clay soil. The RDA axis I displays 66.0% and axis II 5.9% of the Apothecia-Survival matrix.

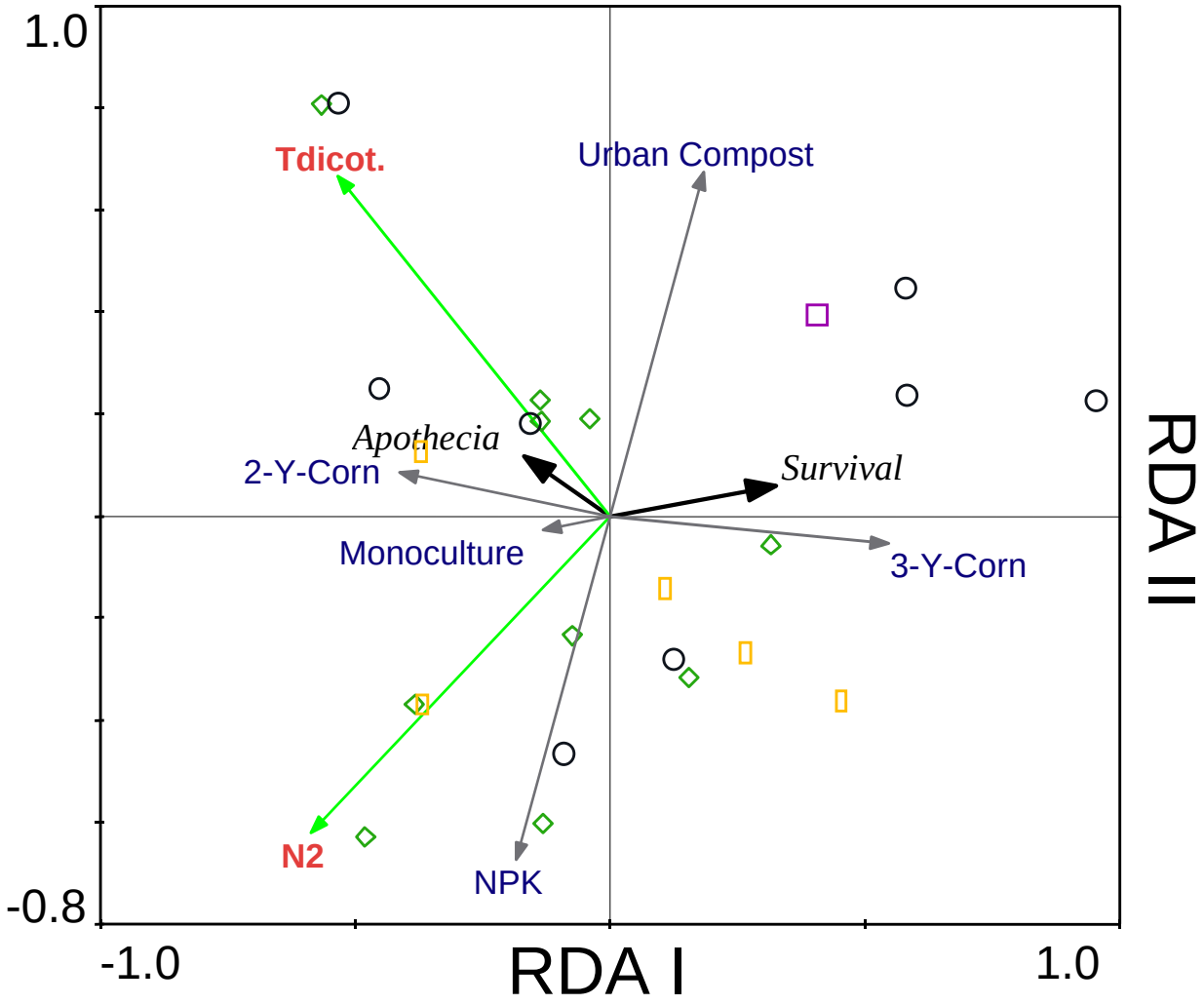

Figure 5b. Clay loam, 2002: partial redundancy analysis (pRDA) correlation triplot of sclerotia survival (*Survival*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by additive forward selection controlling for space (model III, P = 0.008). Abbreviations of variables and treatments are given in Fig. 1. The treatments rotation and fertilization are included as passive variables in the analysis. Samples are classified by soil type: ○ Sand-clay loam; ▯ Sand-clay soil; ◊ Clay loam; □ Clay soil. The RDA axis I displays 6.7% and axis II 0.9% of the Apothecia-Survival matrix.

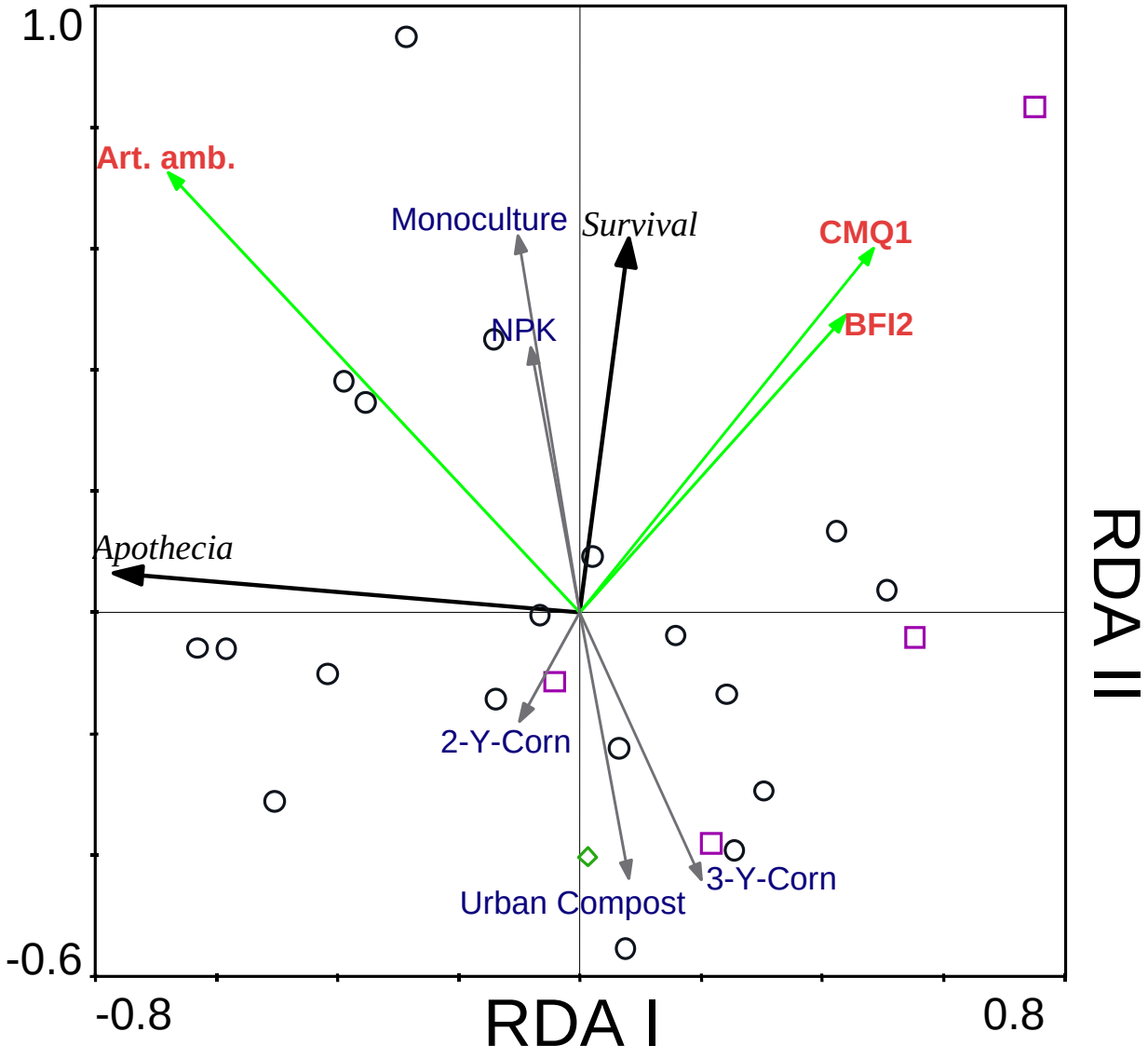

Figure 6a. Sandy loam, 2002: redundancy analysis (RDA) correlation triplot of sclerotia survival (*Survival*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by additive forward selection (model I, $P = 0.001$). Abbreviations of variables and treatments are given in Fig. 1. The treatments rotation and fertilization are included as passive variables in the analysis. Samples are classified by soil type: ○ Sandy loam; □ Loamy sand; ◊ Sand-clay soil. The RDA axis I displays 29.9% and axis II 19.2% of the Apothecia-Survival matrix.

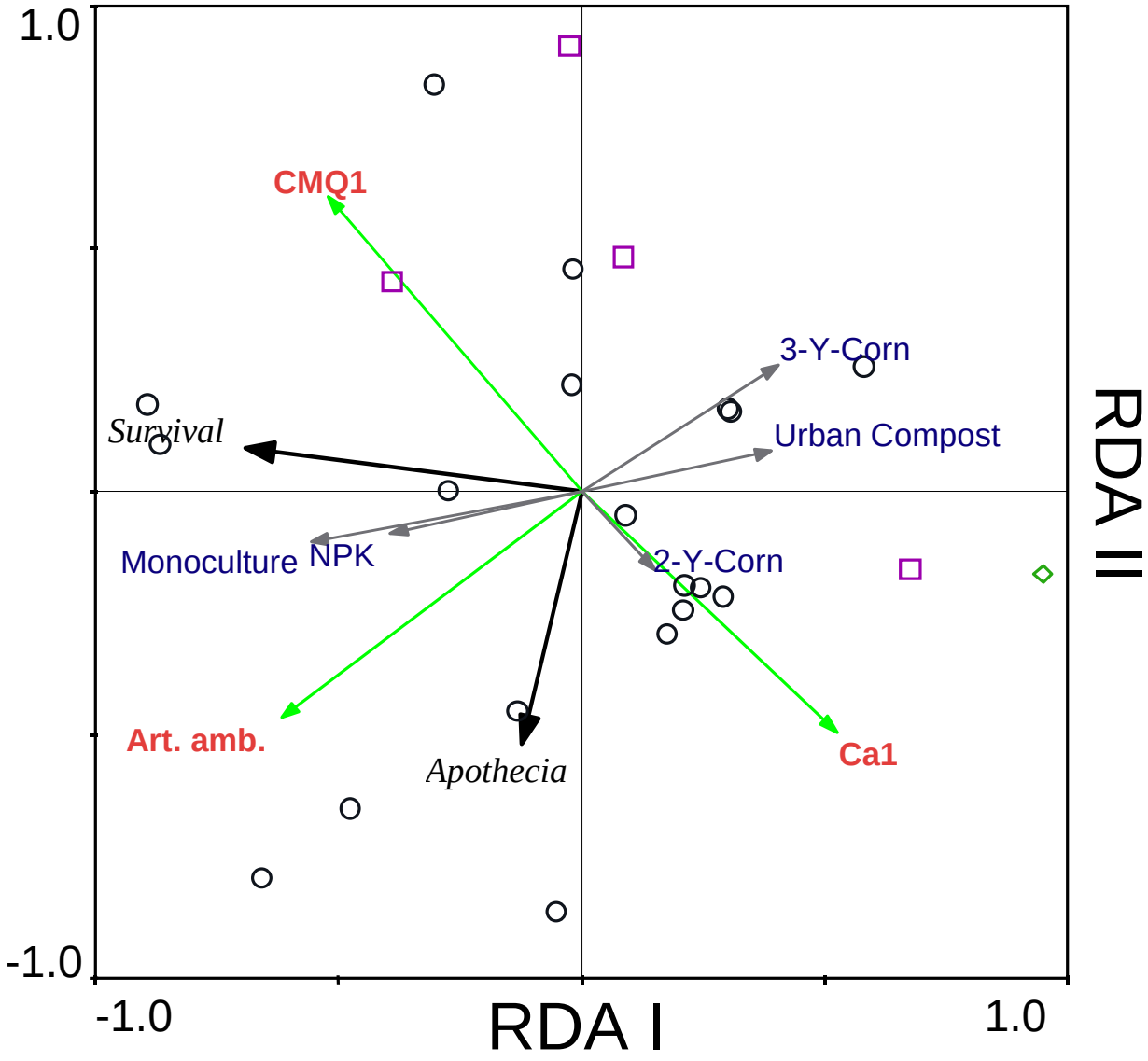

Figure 6b. Sandy loam, 2002: partial redundancy analysis (pRDA) correlation triplot of sclerotia survival (*Survival*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by forward selection controlling for space (model III, P=0.001). Abbreviations of variables and treatments are given in Fig. 1. The treatments rotation and fertilization are included as passive variables in the analysis. Samples are classified by soil type: ○ Sandy loam; □ Loamy sand; ◊ Sand-clay soil. The RDA axis I displays 50.2% and, axis II 35.5% of the Apothecia-Survival matrix.

CHAPITRE 3. Partition de la variation spatiale et environnementale de la sclérotiniose du soja

Sommaire: Dans le chapitre 2 précédent, des modèles minimaux ont regroupé les variables qui expliquent le mieux les variables de sclérotiniose (*Sclerotinia sclerotiorum*) du soja. Au site argileux, la rotation 3 ans de maïs a réduit la gravité de la maladie (DSI) notamment par la réduction de la biomasse des adventices. Le compost urbain a favorisé la gravité de la maladie et la survie des sclérotes dans ce sol, effets expliqués par le drainage. Au site sableux, la germination carpogénique était corrélée négativement à un quotient de minéralisation du C et à une stabilité des agrégats plus élevés, alors que la germination était corrélée positivement avec la teneur en Ca. À l'opposé, la survie des sclérotes était corrélée négativement à la présence de Ca. Dans le présent chapitre 3, la variance de la survie des sclérotes, de leur germination carpogénique et de la gravité de la sclérotiniose a été séparée, dans les deux sols (loam argileux et loam sableux), entre quatre matrices: couvert végétal, physico-chimie et microbiologie du sol, pratiques culturales (rotations 2-3 ans de maïs / monoculture de soja et fertilisation minérale / compost urbain) et espace. La régression multiple et l'analyse canonique des redondances partielles ont été utilisées pour la partition de la variance des variables de sclérotiniose individuellement, ou en association: DSI-Apothécies et Apothécies-Survie. Au site argileux, la variance de la survie des sclérotes et du nombre d'apothécies était expliquée par la structure spatiale des variables physico-chimiques du sol, i.e. la texture et la structure du sol conditionnaient la survie et la germination carpogénique. La variance du DSI ne partageait pas cette structure spatiale et était expliquée par les effets de la rotation (3 ans de maïs) sur le couvert végétal et la physico-chimie du sol: la rotation a réduit la biomasse des adventices, diminuant ainsi le nombre d'apothécies, et a amélioré le rendement du soja. Au site sableux, la variance du DSI a été principalement expliquée par la structure spatiale du couvert végétal et de la physico-chimie du sol. La réduction de la maladie par l'interaction de la rotation de 3 ans de maïs et du compost urbain a été expliquée par une meilleure stabilité des agrégats, une plus forte activité microbiologique et une concentration de la solution du sol en ions échangeables plus élevée et corrélée négativement à la production d'apothécies. La survie des sclérotes a semblé au contraire être favorisée par cette amélioration des propriétés du sol. Pour la première fois, la partition de variance des variables de sclérotiniose entre quatre matrices de variables spatiales et environnementales a

permis d'interpréter et de quantifier la variance expliquée par les effets des pratiques culturales sur la maladie et leurs interactions avec les principaux facteurs qui caractérisent cet agroécosystème.

Mots clés: analyse canonique des redondances (partielle), couvert végétal, microbiologie du sol, partition de variance, pratiques culturales, *Sclerotinia sclerotiorum,* soja.

Partitioning the spatial and environmental variation of *Sclerotinia* stem rot on soybean

Abstract: The variance in survival of *Sclerotinia sclerotiorum*'s sclerotia, carpogenic germination (Apothecia) as well as *Sclerotinia* stem rot (SSR) severity (DSI) on soybean was partitioned among canopy, soil physico-chemistry and microbiology, cultural practices (2-3-y-corn rotation/soybean monoculture and mineral fertilization/urban compost), and spatial matrices in two soils. Partial multiple regression was used to partition the individual SSR variables variance while partial canonical redundancy analysis partitioned the DSI-Apothecia and Apothecia-Survival variance. In clay loam, the sclerotia survival and apothecia variance was mainly explained by the spatial structure of soil physico-chemistry while the disease severity variance did not share this spatial structure and was largely explained by the effects of 3-y-corn rotation on canopy and soil, i.e. lower weed biomass, enhanced soybean yield and fewer apothecia were correlated with disease suppressiveness. In sandy loam, the DSI variance was mostly explained by the spatial structure of canopy and physico-chemistry. Disease suppressiveness, by the interaction of 3-y-corn rotation with urban compost, was largely explained by the enhancement of soil properties, i.e. higher aggregate stability, microbial activity and soil solution concentration in exchangeable ions correlated negatively with carpogenic germination. Partitioning the SSR variance among four matrices of spatial and environmental factors allowed for the first time to interpret and quantify the variance of disease development explained by cultural practices in interaction with the main characteristics of this agroecosystem.

Key words: (partial) canonical redundancy analysis, cropping practices, plant canopy, *Sclerotinia sclerotiorum*, soil microbiology, variance partitioning, soybean.

Introduction

The *Sclerotinia* stem rot (SSR) of soybean (*Glycine max* L.), caused by the soil-borne discomycete *Sclerotinia sclerotiorum* (Lib.) de Bary, is one of the principal diseases of soybean plants in Northeastern America (Anderson and Tenuta, 2001). Little is known about the ecology of *S. sclerotiorum* and soil-borne pathogenic fungi particularly because their relationships with soil and hosts are complex and diverse (Lazarovits, 2001). For example, the relative success of antagonists (Tokeshi et *al.*, 1997) or organic amendments (Asirifi et *al*., 1994; Ferraz et *al*., 1999; Viana et *al.*, 2000) used to suppress soil-borne diseases are often limited by the lack of understanding the complex interactions involved (Lazarovits, 2001). Reeleder (2003) explored the present development of molecular techniques allowing the characterization of soil communities. Such tools aid in understanding and predicting the response of plant pathogens to the application of a biological control agent or of an organic amendment. Molecular tools such as the use of PCR primers developed for the quantification of *S. sclerotiorum*'s ascospore inoculum may aid in the development of a risk management strategy for soybean SSR (Freeman et *al*., 2002). In addition, there is a need for the adoption of a systemic approach in research that would allow to achieve a more global understanding of the dynamics between soil-borne pathogens and their ecosystem. In this light, the use of the multivariate statistics developed mainly for numerical ecology is important. Bailey et *al*. (2001) used principal component analysis (PCA) and canonical discriminant analysis (CDA) to explain the development of wheat and pea foliar diseases as a result of crop rotation and tillage. Such a multivariate approach allowed these authors to combine the results of six years of crop sequences, a feat that cannot be achieved by classical univariate approaches (ANOVA). Bailey et *al*. (2001) were thus able to establish over a relatively long period of time, that crop rotation and tillage did not substantially affect the foliar and root disease intensity but that rotation and tillage modified the ecology of wheat and pea soil-borne or residue-borne foliar disease agents. Such an experiment was original in plant pathology as it demonstrated the power of multivariate analyses to study the long term dynamics of these primary foliar disease agents in the Canadian prairies. It also confirms that the use of diversified rotations and no-till practices are economically viable for growers in this region. As there is a lack of data on systemic studies of SSR and its relationship with soil and crop cover in Québec, there is little possibility of developing either disease developmental models nor risk management systems (Mila et *al*., 2003) that could serve to predict disease

occurrence or intensity (Bom and Boland, 2000). These models would be helpful in the development of adequate measures of control of SSR outbreaks on soybean crops.

In the present study which was conducted in Saint-Hyacinthe, Québec (Canada), between 1999 and 2002, the effects of corn-soybean rotations, and of fertilization using urban compost or conventionnal mineral fertilizer or a combination of both, were studied. With the help of multivariate statistics, the relationship of SSR variables in response to rotation and fertilization treatments as well as to a total of 69 variables characterizing soil and crop canopy were investigated. Results of this field experiment are presented in a total of three chapters, this one being the third.

At first, the results of Chapter 1 showed how crop rotation combined with fertilization, using urban compost or conventional mineral fertilizer, affected the severity of SSR on soybean, the production of apothecia, and the survival of sclerotia of *S. sclerotiorum*. Chapter 2 focused on the effects of soil and plant canopy variables on these *Sclerotinia* stem rot variables and their interactions with the rotation and fertilization treatments. An additive approach was used to construct regression and RDA models containing minimal sets of explanatory variables (Pinel-Alloul et *al*., 1995).

The results of chapters 1 and 2 concerning rotation and fertilization effects, generally supported the results previously observed by authors who had also studied soil-borne pathogens. Kurle et *al*. (2001) and Garcia-Garza et *al*. (2002) reported that rotation with a non-host crop contributed to the reduction of disease severity compared to monoculture, and that this was especially true when reduced tillage or no-till was also applied. As suggested by Alexander and Stewart (1994), rotation alone was not generally able to reduce or control *Sclerotinia* disease development due to the fact that a small number of persistent sclerotia may initiate a new disease cycle at the end of a rotation. The results of Chapter 1 reported that the 3-y-corn rotation significantly reduced disease incidence in clay loam and also in sandy loam but only in combination with the use of an urban compost amendment. However, crop rotation and organic amendment did not affect carpogenic germination in both soils studied. In addition, urban compost may significantly enhance sclerotia survival in clay loam (in one out of 3 years). Ferraz et *al.* (1999) reported similar disease conduciveness caused by organic amendments, but did not attributed it specifically to sclerotia survival enhancement.

Chapter 2 served to identify key variables that explained the development of the SSR disease. The regression and redundancy analyses (Legendre and Legendre, 1998) showed that in clay loam, while

weed variables directly affected carpogenic germination, weed variables did not directly impact disease severity, whose variation was rather explained by the 3-y-corn rotation. In sandy loam, the interaction 3-y-corn x Urban Compost reduced disease severity both directly and indirectly through the weed biomass reduction. In sandy loam, a negative correlation between wet aggregate stability, soil biological activity (carbon mineralization quotient) and carpogenic germination was identified. The opposition between carpogenic germination and aggregate stability was also observed to a lesser extent in clay loam and was already reported by Tokeshi et *al.* (1997) as a possible suppressive factor of *Sclerotinia minor*'s sclerotia that interacted with biological activity. This was also reported by Lumsden et *al*. (1986) for lettuce drop caused by *Sclerotinia minor*. These authors also identified the soil nutrient status as a factor involved in *Sclerotinia* suppression.

The use of multiple regression, redundancy analysis and their partial forms, allowed to identify for the first time key variables that drive the development of *Sclerotinia* stem rot on soybean. As a result, it is possible to propose new hypotheses on the relationships of SSR variables with cultural practices such as crop rotation with non-host crops or the use of organic amendments. For the first time, it was possible to generate multivariate models that can be tested for significance and that allow to interpret relations between rotation and fertilization on the one hand, soil and plant canopy variables as well as the spatial structure of the data on the other hand (Chapter 2).

The next step in this study consisted of the use of the partial forms of regression and redundancy analyses to partition the variation of *Sclerotinia* stem rot variables between each set of spatial, environmental (canopy, soil physics, chemistry and microbiology) and rotation and fertilization variables (Borcard et *al*., 1992; Legendre, 2003; P. Legendre, pers. com.). The most discriminant variables of each set were selected using the forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002) prior to variance partitioning. The variance partitioning had three objectives: i) to quantify marginal and conditional fractions of the variance in SSR variables which could be explained by rotation and fertilization treatments and each set of spatial or environmental variables (marginal fraction refers to the fraction of each set used alone in the analysis while the conditional fraction refers to the remaining variance when one or more sets are treated as covariables); ii) to quantify the variance fractions of SSR variables which could be jointly explained by all combinations of treatments and sets of spatial or environmental variables; iii) to synthesize the information given by the variance partitioning and the additive selection developed in Chapter 2, in

order to better explain interactions between SSR, rotation and fertilization treatments, and the environment considering spatial autocorrelation (Legendre and Troussellier, 1988).

Materials and Methods

Experimental design and data collection

The study site, field history, experimental design, disease assessments, soil and compost physico-chemical analyses are detailed in Chapter 1; soil microbiology and plant canopy in Chapter 2. The treatments and environmental variables and their abbreviations, the units and references on methods used are given in Table 1.

Statistical analyses

Normality of data was tested using PROC CAPABILITY procedure of the Statistical Analysis System (SAS Institute Inc., 2001), and homogeneity of variances was examined by plotting residuals versus predicted values using the PROC GLM and PROC PLOT procedures. Non-normal variables were previously transformed using appropriate transformations (Underwood, 1997).

To partition the variation explained by spatial variables, environmental variables and rotation and fertilization treatments on DSI, apothecia number, sclerotia survival and their combinations, multiple linear regression, canonical redundancy analysis (RDA) and their partial forms (Borcard et *al*., 1992) were used. Two SSR variables combinations were studied: DSI-Apothecia was defined as the aerial matrix while Apothecia-Survival was defined as the soil matrix. As the main interest holds in studying the interactions of rotation and fertilization treatments with each set of spatial or environmental variables, only the results of year 2002 will be presented.

By multiple linear regression, the partial RDA (pRDA) allows to remove the effect of one or more variables whose effect is well known or undesired. To select the variables within each set of environmental (phenology and weeds; soil physics; soil chemistry; soil microbiology) and spatial variables which may explain a significant fraction of the SSR variables and their combinations, the forward selection procedure of CANOCO 4.5 (Microcomputer Power, 2002) was computed separately on each variable set. This first selection was called the "independent selection" (Pinel-

Alloul et *al*., 1995). As the two fields were not homogeneous regarding to soil type classification, six binary soil type variables were created: sandy loam (SL), loamy sand (LS), sand-clay loam (SCL), sand-clay (SC), clay loam (CL), and clay soil (CS). All the soil variables (physics, chemistry and microbial activity) were labeled $_1$ when they were measured in A_1 (0-10 cm), and labeled $_2$, when they were measured in A_2 (10-20 cm). The variables are summarized in Table 1. The matrix of spatial variables consisting of two-dimensional geographical coordinates, x and y located in the center of each plot, was produced by adding all terms for a cubic trend surface regression of the form:

$$\hat{z}=b_1x+b_2y+b_3x^2+b_4y^2+b_5x^3+b_6y^3+b_7xy+b_8x^2y+b_9x^3y+b_{10}xy^2+b_{11}xy^3+b_{12}x^2y^2+b_{13}x^2y^3+b_{14}x^3y^3.$$

The 14 terms of the equation were submitted to the forward selection procedure as were the sets of environmental variables (Borcard et *al*., 1992). At each step, the forward selection procedure selects the variable that adds the most to the explained variability in the response data (SSR variables). The contribution of each added variable is tested by Monte Carlo permutations test, with 999 permutations.

Multivariate analyses specific to this chapter

The canonical axes of the model resulting from selection are also tested by permutations (ter Braak and Smilauer, 2002). In the procedure, all the variables with a probability level $P < 0.15$ are kept only if the next variable included in the model has a probability level $P < 0.05$. If no such variable is retained, only variables with probability level $P < 0.10$ are kept to build the models. The models selected by the procedure are significant at the probability level $P < 0.05$. The models represent the marginal fraction of variance explained by each set of environmental variables. The marginal fraction is referred to as the fraction of variance explained in the response matrix, when one set of environmental variables is used alone in the analysis. The partitioning is used to determine the conditional fraction of each set of variables; the conditional fraction is the fraction of response matrix variance explained by one set (or group of sets) after removing the fraction of variance explained by an other set (or group of sets) of variables (Legendre and Legendre, 1998).

The resulting sets of spatial and environmental variables, along with the variables that coded for the significant rotation and fertilization treatments, were used in the variance partitioning. The treatments (rotation and fertilization) were coded by dummy variables as described by Legendre and

Anderson (1999) and submitted to the two-way ANOVA (MANOVA) design whose results were presented in Chapter 1. The partioning was computed with the Program for partitioning the variation of a response table Y among 1, 2, or 3 explanatory tables X, developed by Legendre (2003). Four matrices were created among the sets that explained a significant amount of SSR variables. The matrices of soil physics, soil chemistry, and soil microbiology were combined to reduce the number of matrices to four, referred to as X1 to X4. Because the program is designed to perform partition with three matrices, three partitionings of Y matrices of SSR variables were performed grouping successively X3+X4, X2+X3 and X2+X4. Then, the necessary 16 fractions of variance (noted [a] to [o]) were calculated by substraction (P. Legendre, pers. com.). Only fractions [a] to [d] and subsets containing fractions [a] to [d] can be tested for significance (five canonical analyses per permutation to test). Fractions [e] to [o] cannot be tested individually (Legendre, 2003). The testable fractions [a] to [d] represent the conditional (pure) fractions of each set of variables. Three subsets containing fractions [a] to [d] were also testable; these three subsets represent the joint variation plus the pure variation explained by two matrices among three of the matrices in the analysis (X1, X3 and X4). These combinations were: X1-X3, X1-X4 and X3-X4. Diagrams were created to illustrate the fractions of variation calculated. Correlation triplots were also produced using CANODRAW (Microcomputer Power, 2002) to illustrate the correlations between the environmental variables selected in each set by forward selection and the SSR variables included in the aerial and soil matrices. In the correlation triplots, the variables for the most explanatory set are included as active environmental variables, while the other variables are included as passive or supplementary variables and therefore are not included in the calculation of the canonical axes.

Results

Forward selection

Multiple regression analyses on individual SSR variables

Disease severity

Results of the forward selection procedure on DSI are shown in Table 2. None of spatial variables explained significant variation in the clay loam site. However, in the sandy loam site, 51.6% of DSI variation ($P = 0.005$) was explained by three spatial variables. Canopy variables explained 61.4% of

DSI variance in clay loam (P = 0.001) and 35.2% in sandy loam (P = 0.013). Yield and LAI1 were retained in the clay loam model, while total weeds and *Amaranthus retroflexus* were in sandy loam. Soil physics explained 46.5% of DSI variation in clay loam (P = 0.009) and 21.3% in sandy loam (P = 0.023). $Silt_2$, OM_1, OM_2, and MWD were retained in clay loam, and only OM_2 was retained in sandy loam. Soil chemistry explained 28.3% of DSI variance in clay loam (P = 0.031) and 49.4% in sandy loam (P = 0.002). Among soil chemistry variables, S_2 and CN_1 were retained in the clay loam model, while C_1, P_2, and CEC_2 were retained in sandy loam. Soil microbiology explained a fraction of DSI variance (29.1%) in the clay loam site only (P = 0.024). Variables $PS1_1$ and $PS1_2$ were retained in the model.

Carpogenic germination

Results of forward selection on Apothecia are shown in Table 3. Spatial variables explained 84.2% of Apothecia variance in the clay loam site with three variables (P = 0.001) and 26.0% in sandy loam, with only one variable (P = 0.009). Canopy variables explained 51.9% of Apothecia variance in clay loam (P = 0.012) and 32.0% in sandy loam (P = 0.011). Total dicotyledons and *Polygonum aviculare* were retained in clay loam, while only *Ambrosia artemisiifolia* was retained in sandy loam. Soil physics explained 48.9% of Apothecia variance in clay loam (P = 0.018) and 52.8% in sandy loam (P = 0.002). The variables MWD, $Sand_1$, CS_2 and SCL_1 were retained in clay loam, while $Clay_1$ and MWD were in sandy loam. Soil chemistry explained 70.2% of Apothecia variance in clay loam (P = 0.002) and 50.4% of the variance in sandy loam (P = 0.007). The variables P_2, Al_2, Ca_1, K_1 and C_1 were retained in analyses on clay loam soil, while Al_1, S_2 and Al_2 were retained for those on sandy loam. Soil microbiology explained 22.0% of Apothecia variance in clay loam (P = 0.037) and 40.8% in sandy loam (P = 0.016). Only $PS1_1$ was retained in clay loam, while $PS1_1$, CMQ_1 and BFI_2 were retained in the sandy loam site.

Sclerotia survival

Results of forward selection on sclerotia survival are shown in Table 4. Spatial variables only explained a significant fraction of the variance in sclerotia survival in the clay loam site (72.8%). This analysis retained three variables (P = 0.001). Similarly, canopy variables explained a significant fraction of Survival variance (33.2%), but only in clay loam (P = 0.028). *P. aviculare* and Total dicotyledons were retained in the model. Again, soil physics explained a significant fraction of Survival variance (69.0%), but only in clay loam (P = 0.001). MWD, $Sand_1$, and $Clay_2$ were retained in this analysis. Soil chemistry explained 51.2% of Survival in clay loam (P = 0.001)

and 30.0% in sandy loam (P = 0.032). The variables N_2 and P_2 were retained in clay loam, while pH_1 and P_1 were retained in sandy loam. Soil microbiology explained 22.5% of the variance in sclerotia survival in clay loam (P = 0.011) and 19.9% in sandy loam (P = 0.024). One single variable was retained in each model: $PS1_2$ in clay loam and BFI_1 in the sandy loam site.

Redundancy analyses on DSI-Apothecia and Apothecia-Survival matrices

The aerial matrix: disease severity and carpogenic germination

In the clay loam site, the DSI and apothecia were slightly positively correlated (r_p = 0.37, P = 0.06). In this clay loam site, Apothecia explained 13.5% of the DSI variance. In the sandy loam site, DSI and Apothecia were not correlated (r_p = 0.21, P > 0.05) (Chapter 1).

Results of forward selection on DSI-Apothecia matrix are shown in Table 5 (Fig. 1a-b). Spatial variables explained 56.7% of DSI-Apothecia variance in clay loam with four variables (P = 0.001) and 19.3% in sandy loam, with one variable (P = 0.01). Canopy variables explained 55.9% of DSI-Apothecia variance in clay loam (P = 0.001) and 24.2% in sandy loam (P = 0.006). Total dicotyledons, *P. aviculare* and Yield were retained in clay loam, while *A. artemisiifolia* was retained in sandy loam. Soil physics explained 33.9% of DSI-Apothecia variance in clay loam (P = 0.005) and 39.7% in sandy loam (P = 0.001). $Silt_2$, OM_1 and OM_2 were retained in clay loam, while $Clay_1$, MWD and SL_2 were retained in sandy loam. Soil chemistry explained 47.0% of DSI-Apothecia variance in clay loam (P = 0.005) and 48.3% in sandy loam (P = 0.001). The variables P_2, Al_1, S_2, and CEC_1 were retained in clay loam, while Al_1, S_2, P_2, and CEC_2 were retained in sandy loam. Soil microbiology explained 18.8% of DSI-Apothecia variance in clay loam (P = 0.024), and 26.1% in sandy loam (P = 0.007). Only $PS1_1$ was retained in clay loam, while $PS1_1$ and CMQ_1 were retained in the sandy loam site.

The soil matrix: carpogenic germination and sclerotia survival

In the clay loam site, Apothecia and Survival were positively correlated (r_p = 0.71, P = 0.003) and Survival explained 50.5% of Apothecia variance. In the sandy loam site, the Apothecia and Survival were uncorrelated (r_p = 0.08, P > 0.05) (Chapter 1).

Results of forward selection on Apothecia-Survival matrix are shown in Table 6 (Fig. 2a-b). Spatial variables explained 77.8% of the variance observed for Apothecia-Survival in clay loam, with three

variables (P = 0.001). It also explained 12.8% of observed variance for Apothecia-Survival in sandy loam with only one variable (P = 0.05). Canopy variables explained 42.6% and 23.8% of the variance observed for Apothecia-Survival in clay loam (P = 0.011) and sandy loam (P = 0.004) respectively. Total dicotyledons and *P. aviculare* were retained in analyses in clay loam while *A. artemisiifolia* was retained in sandy loam. Soil physics explained 42.9% and, 20.8% of the variance observed in clay loam (P = 0.013) and in sandy loam (P = 0.006) respectively. CL_2, $Clay_1$, and MWD were retained in clay loam, while $Clay_1$ was retained in sandy loam. Soil chemistry explained 52.4% and 62.8% of the variance observed in Apothecia-Survival in clay loam (P = 0.002) and in sandy loam (P = 0.003) respectively. P_2, N_2, and Al_2 were retained in analyses in clay loam while Al_1, Ca_1, CN_1, and P_2 were retained in analyses for sandy loam. Soil microbiology explained 22.0% and 47.0% of the variance in Apothecia-Survival in clay loam (P = 0.007) and in sandy loam (P = 0.001) respectively. Only $PS1_2$ was retained in clay loam, while CMQ_1, $PS1_1$, $PS2_1$, and BFI_2 were retained in the sandy loam site.

Variance partitioning

Variance partitioning of individual SSR variables

Disease severity

In the clay loam site (Fig.3a), variance in the DSI was partitioned by four matrices of treatment and environmental variables that jointly explained 87.4% of total DSI variance (P = 0.002). The four matrices retained in the analysis were: rotations, canopy, soil physico-chemistry, and soil microbiology. Spatial variation was not a significant factor in disease severity for clay loam. Neither the four conditional fractions of treatments or environmental matrices nor the subsets formed by the combinations of two of the matrices were significant. The variation explained by the rotations (36.4%) was jointly explained with canopy (16.4%), canopy plus physico-chemistry (13.0%), all other matrices (7.4%), and microbiology (3.2%). The pure fraction of DSI variation explained by rotation was only 2.4%. The total DSI variation explained by canopy (61.4%) was common mainly with rotation and physico-chemical variables (33.5%). The pure canopy fraction was 7.3%. The fraction of DSI variation explained by soil physico-chemical variables (55.2%) was jointly explained with canopy and microbiology (13.4%), canopy and rotations, all other matrices, microbiology (6.3%), and canopy alone (4.1%). The pure fraction of DSI explained by soil physico-chemistry was the highest with 14.5%. The pure microbiology fraction was 3.2%. The testable

subset (pure plus conjointly explained variation of two matrices) of rotations with soil physico-chemistry explained 17.4% of the variance observed in the DSI, the subset of rotations with microbiology 8.7%, and the subset of physico-chemistry with microbiology, 24.0%.

In the sandy loam site (Fig. 3b), the variance observed in the DSI was partitioned by four matrices of treatments, spatial and environmental variables that jointly explained 75.8% of total DSI variance ($P = 0.03$). The four matrices retained in the analysis were: interaction rotation x fertilization, space, canopy, and soil physico-chemistry. Soil microbiology did not account for a significant amount of DSI variance in the sandy loam site. None of the four conditional fractions of treatments, space, environmental matrices, and the testable subsets of two matrices were significant. The variation explained by the interaction (14.8%) was jointly explained with soil physico-chemistry (8.1%), space plus physico-chemistry (3.3%), and all other matrices (2.3%). The pure fraction of DSI variance explained by the rotation x fertilization interaction was of 3.3%. The entire canopy fraction was jointly explained by other matrices: 23.0% was jointly explained with space plus physico-chemistry, space alone (11.4%), all other matrices (2.3%) and soil physico-chemistry (1.1%). The canopy accounted variance was most spatially structured having no pure component. The total DSI variance explained by soil physico-chemistry (50.1%) was mostly "spatialized" and common with all other matrices, particularly that of canopy. The total variance explained jointly by physico-chemical matrix, other environmental matrices and space was of 25.3%. The common fraction of explained variance with space only was of 1.2%. The pure physico-chemistry explained variance was of 11.4%. The strictly spatial DSI variance was of 12.6%. The subset that contains the pure and common fraction of the interaction and physico-chemistry explained 22.8% of DSI variance. The subset containing canopy and physico-chemistry explained 12.8% and the interaction-canopy subset explained 4.0%.

Carpogenic germination

In the clay loam site (Fig. 4a), the variance of Apothecia was partitioned by four matrices of spatial and environmental variables, that jointly explained 96.7% of the variance of Apothecia ($P = 0.001$). The four matrices retained in the analysis were space, canopy, soil physico-chemistry, and soil microbiology. The treatments were not significant factors in clay loam (Chapter 1). The pure fraction of spatial variability was a significant factor ($P = 0.03$) in contrast to the other pure fractions. Two of three testable subsets explained a significant amount of Apothecia variance. These subsets consist of: space-physico-chemistry ($P = 0.01$) and space-microbiology ($P = 0.03$). The

subset physico-chemistry-microbiology was not significant. The total spatial variability (86.6%) was for the most part shared with the other matrices or their combinations (76.6%). The joint variance accounted for by space and physico-chemistry was of 22.0%. The joint variance explained by physico-chemistry and canopy or with all other matrices was of 31.5% and 11.4% respectively. Therefore, the factor canopy explained 51.9% of the Apothecia variance. This canopy factor was mostly spatially structured (46.4%) and jointly shared with physico-chemistry or microbiology (2%) or with both. The joint variance between canopy and space along with the shared variation with physico-chemistry explained the only low variance values of 1.5% and 3.5% respectively. The pure canopy variance was only 2.0%. The variance explained by the physico-chemistry and microbiology matrices were generally spatially structured and showed an interaction with other matrices. The significant subsets of space-physico-chemistry, and space-microbiology explained 36.3% and 13.2% respectively of the Apothecia variance observed in the clay loam site. The subset physico-chemistry-microbiology explained 4.9% of the Apothecia variance observed.

In the sandy loam site (Fig. 4b), the variance in Apothecia was partitioned by four matrices of spatial and environmental variables, that jointly explained 82.2% of Apothecia variance ($P = 0.003$). The four matrices retained in the analysis were space, canopy, soil physico-chemistry and soil microbiology. The treatments (rotation and fertilization) were not significant factors in the sandy loam site (Chapter 1). The variance explained by the pure fraction of physico-chemistry was significant ($P = 0.05$) while the other pure fractions were not. The variance of Apothecia explained by the subset physico-chemistry-microbiology was significant ($P = 0.01$), but not that explained by subsets space-microbiology and space-physico-chemistry. The total variance explained by physico-chemistry was of 69.5% and represented the most important matrix. It shared explained variation mainly with all other matrices (20.9%), with canopy (18.5%), microbiology (14.2%), and with space-microbiology (8.0%). The variance explained by the pure physico-chemistry factor was of 21.3%. The microbiological matrix was the second most important (40.8%) and most of its explained variation was shared with all other matrices, the physico-chemistry or space-physico-chemical matrix. The pure microbiology fraction explained 7.8% of the observed variance. Canopy explained 32.3% of the variance and was entirely shared with other matrices but especially with all other matrices and physico-chemistry. Canopy matrix was the most spatially structured matrix with 23.9% of variance jointly explained with space alone or space plus all other matrices. Spatial variance (25.7%) was mainly shared with other matrices, with a pure spatial fraction of 6.2%. The testable subset physico-chemistry-microbiology explained 43.3% of Apothecia variance while the

subset space-microbiology and the subset space-physico-chemistry explained 11.9 and 21.9% of the observed variance respectively.

Sclerotia survival

In the clay loam site (Fig. 5a), the Survival variance was partitioned by four matrices of spatial and environmental variables, that jointly explained 89.1% of the Survival variance ($P = 0.003$). The four matrices retained in the analysis were space, canopy, soil physico-chemistry, and soil microbiology. The treatments were not significant factors in clay loam (Chapter 1). No pure fraction was significant in the clay loam site. The variance explained by subset space-physico-chemistry was significant ($P = 0.008$), but not the variance explained by the subsets physico-chemistry-microbiology and space-microbiology. The total variance explained by physico-chemistry (80.7%) was the most important and was shared mainly with space and canopy (26.6%), space and microbiology (19.2%), and space alone (16.8%). The pure fraction of physico-chemistry explained 12.0% of the observed variance. Spatial variability was the second most important component of Survival variance (72.8%) and was mostly shared with the variance of other matrices (66.8%). The pure spatial fraction explained 5.7% of the observed variance. Canopy explained variation was entirely shared with other matrices: space-physico-chemical matrices (26.6%), physico-chemical matrix alone (2.3%), all other matrices (2.2%), and space alone (2.0%). The variance explained by microbiology was also entirely shared with space-physico-chemistry (19.2%), all other matrices and physico-chemistry alone (1.7%). The testable subset space-physico-chemistry explained 34.5% of the Survival variance while the subset physico-chemistry-microbiology and the subset space-microbiology explained 13.7 and 6.2% respectively.

In the sandy loam site (Fig. 5b), the Survival variance was partitioned by two matrices of environmental variables that jointly explained 51.5% of the Survival variance ($P = 0.003$). The two matrices retained in the analysis were soil chemistry and soil microbiology. The treatment effects were not significant in the sandy loam site (Chapter 1). The pure fractions of both chemistry (31.3%) and microbiology (16.6%) were significant ($P = 0.003$ and $P = 0.02$, respectively). The common fraction of explained variance (3.5%) was not testable for significance.

Variance partitioning of the DSI-Apothecia and Apothecia-Survival matrices

The aerial matrix: disease severity and carpogenic germination

In the clay loam site (Fig. 6a), the DSI-Apothecia variance was partitioned by four matrices of treatments, spatial and environmental variables that jointly explained 93.8% of the DSI-Apothecia variance (P = 0.02). The four matrices retained in the analysis were treatments (rotations and fertilization), space, canopy and soil physico-chemistry-microbiology pooled in a sole matrix, the "PCM matrix" (Fig. 6a and b). Neither pure fractions nor testable subsets explained a significant amount of DSI-Apothecia variance in clay loam. Rotations and fertilization explained variance (30.5%) was mostly shared with canopy and soil matrix (8.0%), and canopy matrix alone (7.2%). It was also shared with all other matrices (5.1%), space matrix alone (1.7%) and the space-canopy matrix (1.3%). The pure fraction explained by treatments was of 5.6%. The soil matrix was the most important matrix (61.1%) and shared the explained variation mainly with the space and canopy matrices (23.6%), the space matrix alone (8.4%), and the treatments-canopy matrix. The PCM matrix was the most spatially structured matrix which explained 37.1% of the observed variance which was shared with either the spatial matrix alone, space-canopy, or all other matrices. The pure fraction explained by the PCM matrix was of 12.2%. The space matrix was the second most important in explaining the DSI-Apothecia variance (56.7%). Most of the spatial variability was jointly explained with the canopy and the PCM matrix, PCM matrix alone, with all other matrices, canopy alone (4.4%), the treatments (rotation and fertilization) (1.7%), and treatments-canopy matrices (1.3%). The pure spatial fraction was of 8.4%. The variance for the canopy matrix (55.9%) was the most shared with the other matrices with only 4.0% of pure explained variance. It was also the second most spatially structured matrix (34.4%) with a spatial structure shared mainly with the following matrices: PCM, all other matrices and the treatment matrix. The testable subset of canopy-PCM matrix explained 18.4% of the DSI-Apothecia variance whereas the subsets of treatments-canopy and treatments-PCM matrix explained 16.8 and 15.6% of observed variance respectively.

In the sandy loam site (Fig. 6b), the DSI-Apothecia variance was partitioned by four matrices; four matrices that jointly explained 72.3% of DSI-Apothecia variance (P = 0.05). The four matrices retained in the analysis were: treatment (rotation x fertilization), space, canopy, and soil physico-chemistry-microbiology pooled in a sole "PCM matrix". Neither pure fractions nor testable subsets explained a significant amount of DSI-Apothecia variance in sandy loam. The rotation x fertilization explained variance (7.7%) was all shared with PCM matrix. Almost all the variance of the canopy

and space matrices was explained jointly with the PCM matrix, with the exception of only 2.0% of the canopy variance. The joint explained variance of PCM matrix was accountable to the space-canopy matrices (14.4%), canopy alone (8.3%), space alone (7.6%) and treatment interaction (rotation x fertilization). The pure PCM matrix variance was of 35.0%. The testable subset of the canopy-PCM matrix explained 45.3% of DSI-Apothecia variance, while the subsets of rotation x fertilization-PCM and rotation x fertilization-canopy matrix explained 43.2 and 2.7% of the observed variance respectively.

The soil matrix: carpogenic germination and sclerotia survival

In the clay loam site (Fig. 7a), the Apothecia-Survival variance was partitioned by four matrices of spatial and environmental variables that jointly explained 93.4% of Apothecia-Survival variance (P = 0.001). The fraction of unexplained variance was of 6.6%. The four matrices retained in the analysis were: space, canopy, soil physico-chemistry and soil microbiology. The effect of treatments was not significant in clay loam (Chapter 1). The pure fraction of spatial variation was significant (P = 0.003), along with canopy (P = 0.02), and physico-chemistry pure fractions (P = 0.006). The microbiology pure fraction was not significant. The three testable subsets were significant in clay loam and included physico-chemistry-microbiology (P = 0.008), space-physico-chemistry (P = 0.001) and space-microbiology (P = 0.003). The spatial matrix (77.8%) was the most important in explaining the variance of Apothecia-Survival in clay loam. The pure fraction was also very important (14.6%); however, most of the spatial variation was shared with other matrices including canopy and physico-chemistry (25.2%), physico-chemistry and microbiology (14.5%), physico-chemistry alone (9.1%), canopy alone (7.6%), as well as all other matrices (6.9%). The physico-chemistry matrix (65.7%) was the second most important matrix with a 11.5% pure fraction of explained variance. All the common fraction was shared with space alone, space-canopy, space-microbiology or all other matrices. The canopy explained variation (42.6%) was also in majority shared with space alone, space-physico-chemistry or all other matrices. The pure canopy fraction was of 4.8%. The microbiology explained variation (22.0%) was shared with space-physico-chemistry or all other matrices. The pure microbiology fraction was very low (1.1%). The testable subsets of space-physico-chemistry, space-microbiology, and microbiology-physico-chemistry explained 35.2, 16.1, and 12.3% respectively of the Apothecia-Survival variance in the clay loam site.

In the sandy loam site (Fig. 7b), the Apothecia-Survival variance was partitioned by four matrices of spatial and environmental variables that jointly explained 84.1% of the Apothecia-Survival variance (P = 0.004). The four matrices retained in the analysis were space, canopy, soil physico-chemistry and soil microbiology. The treatments were not significant in sandy loam (Chapter 1). The pure fraction of the Apothecia-Survival matrix explained by microbiology was significant (P = 0.05). However, the pure fractions of space, canopy or physico-chemical matrices were not significant. The testable subset of physico-chemistry-microbiology explained a significant amount of Apothecia-Survival matrix (P = 0.02) while the two other subsets of space-physico-chemistry and space-microbiology were not. Soil physico-chemistry explained the highest fraction of Apothecia-Survival variance (63.3%) with the largest pure fraction (27.1%). The common variance was shared with microbiology (10.7%), canopy (7.6%), canopy and microbiology (7.0%) as well as all other matrices (6.7%). Microbiology had the second largest fraction of explained variation (47.0%) and pure fraction (17.1%). The common explained variance was shared with physico-chemistry, canopy-physico-chemistry, all other variables, space-physico-chemistry (5.3%) and canopy only (1.4%). All canopy explained variation (23.8%) was shared with physico-chemistry, physico-chemistry-microbiology, all other matrices, and microbiology only. The spatially structured variation was low (12.8%) with a pure fraction of 3.0%. The testable subsets of physico-chemistry-microbiology, space-physico-chemistry and space-microbiology explained 54.8, 28.5, and 18.7% of Apothecia-Survival variance respectively in the sandy loam site.

Discussion

Methodology

The variance partitioning approach was complementary with the additive approach previously used to explain SSR variation in Chapter 2. While the additive approach focused on the variables, variance partitioning focused on factors or sets of variables. The additive approach reduced the entire set of variables to the minimum non-redundant information; in this (additive) approach, when two variables are colinear, only the variable that explains the highest significant fraction of variation is retained in the model. The construction of the global non-redundant set was achieved by the pooling in the analyses of all the variable sets previously constructed by independent forward selection (ter Braak and Smilauer, 2002) (D. Borcard, pers. com.). The variables selected helped to

accept or reject the hypotheses that stated the suppressive effect of organic matter amendment, to explain the phenomena involved, and to construct new hypotheses about the role of the variables highlighted (Chapter 2). In the variance partitioning, the analyses were performed on the entire sets of variables selected by the forward selection; the variable sets were not pooled and consequently the redundant, or colinear, variables among sets were not removed. This approach allowed: 1) to focus on the interaction between variable sets or factors; 2) to explain more precisely the role of these ecosystem components on the development of the disease; 3) to quantify the variance explained by the factors and interactions. Such information is helpful for better understanding of the ecosystem or agrosystem functions or to create new hypotheses. Original interpretations of the phenomena may be proposed in a more global view of the SSR disease development in this agrosystem. Thus, variance partitioning provided a quantitative approach that aimed to better explain the contribution of each environmental factor to SSR disease development. It was also aimed to exploit this approach of applied and fundamental ecology (Borcard et *al*., 1992; Pinel-Alloul et *al*., 1995; Weigel et *al*., 2003; Ysebaert and Herman, 2002), in plant pathology.

A limit to variance partitioning in phytopathology emerged early in this study : the need to identify the nature of the relationships between environmental and SSR disease variables. Indeed, it appeared necessary to first perform an additive approach to identify the key variables of each factor involved and to explain or to hypothesize the nature of their relations with the disease variables. The combination of multiple regression and RDA may appear somewhat laborious to promote cultural practices readily available for the growers. However, it is vital to point out the lack of long-term experiments in agriculture. Long-term experiments are essential to efficiently study cultural practices in the perspective of sustainable development. The example of *Sclerotinia* stem rot of soybean is particularly crucial as the fungus is able to survive up to eight years in the soil (Ben Yephet et *al*., 1993) and is also able to initiate a disease cycle with a very low quantity of viable sclerotia (Schwartz and Steadman, 1978).

Variance partitioning

Variance partitioning of individual SSR variables

In the clay loam site (Fig. 3a), the effect of rotation was largely explained by the soybean canopy as the main variable included in the canopy model was soybean yield (Table 2). The disease severity was associated with the cultural practices that offered the lowest yields, this in contradiction with

the results of Mila et *al*. (2003) who reported the association of higher disease incidence with the higher yields. However, these authors did not specify the disease level they encountered. In the present situation, disease severity was high, and when controlling for the effect of rotation, the pure fractions of other factors, alone or combined, were not significant. It was then concluded that the rotation allowed higher yields by drastically reducing the disease severity (Chapter 1). Moreover, this reduction of disease severity was reached mainly through the interaction of rotation with the soil "PCM" (physico-chemistry and microbiology) and the canopy factors (weed biomass reduction).

In the sandy loam site (Fig. 3b), no pure fractions were significant and the 3-y-corn x Urban Compost interaction effect was mainly shared with soil physico-chemistry which suggested that the interaction reduced disease severity essentially through its effect on soil characteristics. The positive correlations of the weed variables and the OM-related variables (OM_2, C_1) with DSI disease index (Table 2) contradict the reduction of disease severity by the 3-y-corn x Urban Compost interaction. However, as observed in the additive model I (Chapter 2), the variables included reflected the variation in DSI attributed to the interaction, then the variables included in Model I were correlated with the 3-y-corn x Urban Compost interaction rather than with DSI directly. This was supported by the additive model II controlling for the interaction effect (Chapter 2). The weed variables effect was almost totally confounded with space and/or soil physico-chemistry (Fig. 3b) which suggested no direct causal relation of weeds with the disease severity and sustained the interpretation of the additive model III controlling for space (Chapter 2). However, even if the weeds were not directly related to disease severity, their presence may have influenced the "microclimatic" conditions under the canopy and then contributed to the disease severity. It is then concluded that the "suppressive" effects of 3-y-corn x Urban Compost interaction was directly related to the soil OM content (urban compost) and indirectly related to the reduction of the density of the canopy by 3-y-corn rotation. The effects of rotation and fertilization treatments were then complementary and suppressive to SSR. In this sandy loam site, only the variance partitioning (Fig. 3b) and model II controlling for the interaction effect (Chapter 2) agreed with the observed suppressive effect of the 3-y-corn x Urban Compost interaction while model I (Chapter 2) and forward selection (Table 2) gave contradictory results. This illustrates the necessity to use different approaches to better understand the interaction involved and the advantages to use the partial form of regression (and RDA) to detect spurious relations that may occur in such complex environment.

In the clay loam site (Fig. 4a), the soil and canopy factors failed to explain all the spatial structure of carpogenic germination (the pure spatial fraction was significant; Fig. 4a). Therefore, the distribution of apothecia in space was a determinant characteristic of carpogenic germination. Boland and Hall (1988b) already reported such a spatial structure which was characterized by a strong aggregation of the apothecia in the field and a significant correlation with the disease development pattern. They suggested that this structure may be important in the development of models for disease prediction. Additionally, the testable subsets that included the pure spatial structure, physico-chemical and microbiology fractions as well as their common fractions, were significant which indicated that the spatial structure of the carpogenic germination was partly confounded with the one of soil physico-chemical and microbiological factors. This was consistent with the assumption made by Boland and Hall (1988b) who related the apothecia spatial patterns with soil factors associated with sclerotia germination such as soil moisture. The forward selection selected soil variables (Table 3) whom most of them were also retained in the forward selection on sclerotia survival (Table 4). In the selection on Apothecia, the contribution of MWD was very high (35%) compared with the additive model III (2%) which suggested that, even if the MWD may induce SSR disease suppression through enhanced soil structure and microbial activity (Tokeshi et *al*., 1997), in a fine textured soil it could also reduce the negative effects of bad drainage that inhibits carpogenic germination (Teo and Morrall, 1985b). The explained fraction of canopy variance was also mainly shared with space-physico-chemical and microbiological characteristics, suggesting that soil characteristics influenced carpogenic germination both directly and in interaction with canopy development. The variance partitioning allowed to support that the spatial pattern of carpogenic germination was determinant alone, but was mainly explained by soil characteristics (Boland and Hall, 1988b). Moreover, it allowed, for the first time, to clearly identify the soil components explaining carpogenic germination and their interactions, with canopy particularly.

In the sandy loam site (Fig. 4b), the situation was pretty different compared with the clay loam site. The carpogenic germination was driven by soil characteristics alone and in interaction with canopy whose variation was entirely shared with the other factors. The spatial pattern was not determinant alone, and was mostly explained by the spatial structure of the soil characteristics (Fig. 4b). This fact may be related to the higher homogeneity of the sandy loam site, particularly in the first soil layer (A_1), but also to the effect of a coarser texture (Table 3) that may allow a better dispersion of sclerotia by till. Again, variance partitioning allowed to better understand the impact of soil

characteristics on the disease development and the importance to realize such experiment in a variety of soils to accurately identify the role of each factor in the disease development. Especially, variance partitioning helped to precise the relations with the variables selected in the additive models (Chapter 2). The carpogenic germination was then stimulated directly by the soil clay content in interaction with *A. artemisiifolia* canopy, while the aggregate stability and/or Al concentration interacted with soil biological fertility (BFI_1) to reduce carpogenic germination.

In the clay loam site (Fig. 5a), the structure of the explained variation of sclerotia survival was quite similar with the one of carpogenic germination. The subset sum of pure and shared spatial and soil physico-chemical fractions was significant and similar (Fig. 5a) to the one observed in Apothecia variation (Fig. 4a) and when analyzing Apothecia and Survival together (Fig. 7a). This suggested that this spatial structure was common to sclerotia survival and Apothecia, as previously reported by Boland and Hall (1988b). The main differences laid in the weaker explanatory power of microbiology (the sum of pure and shared fractions with space was not significant) and canopy, which is not surprising regarding the relative isolation of the sclerotia from the aerial influence of canopy. However, the low influence of microbiology noticed in sclerotia survival was more surprising but supported the results of the additive models (Chapter 2) where no microbiology variables were included contrary to the forward selection results (Table 3, 4 and 6). Therefore, it was not clear if a direct causal link existed between soil microbiology and sclerotia survival, or if these variables only shared a common variation in space and with the soil physico-chemical characteristics (Fig. 4a and 5a). As the present analysis showed that the explained soil microbiology variation was mostly confounded with soil physico-chemical effect, and was almost entirely spatialized, it may be concluded that no direct link could be identified between soil microbiology and sclerotia survival.

In the sandy loam site (Fig. 5b), the sclerotia survival variance was hardly explained by the factors included. As the soil chemistry variables were not strongly correlated with sclerotia survival (Table 4) and were negatively correlated with BFI_1 in the additive models, as well as in the PCA analysis (Chapter 2), it should be hypothesized that the "suppressive" effect identified in the additive models was only apparent: the chemistry variables (pH_1 and P_1; Table 4) were negatively correlated with BFI_1, previously included in the forward selection (Table 4), which was positively correlated with sclerotia survival. Thus no direct causal relationship between survival and chemistry variables were likely to occur. As a consequence, the role of soil chemistry on sclerotia survival in the sandy loam

site was not identified, but the microbial activity, as measured by BFI_1 showed a much clearer trend of "conduciveness" for sclerotia survival (Table 4) (Chapter 2). As a conclusion, no suppressive effect on sclerotia survival was induced by the treatments in this soil. However, the opposite effect of BFI on sclerotia survival and carpogenic germination suggested that a reduction of carpogenic germination by enhanced soil fertility (as measured by BFI_1) induced a higher sclerotia survival since after carpogenic germination the sclerotia naturally die (Mitchell and Wheeler, 1990).

Variance partitioning of the DSI-Apothecia and Apothecia-Survival matrices

The aerial matrix

In the clay loam site (Fig. 6a), the rotation and fertilization effects were mostly confounded with canopy and/or soil physico-chemistry, with relatively low proportion of the variance "spatialized" (8.7%). The canopy was then the most explanatory factor of the rotation and fertilization treatment effects and the variables retained were the weed variables associated with carpogenic germination (Table 3 and 5). It was then concluded that the weed canopy indirectly enhanced carpogenic germination by creating better microclimatic conditions (Schwartz and Steadman, 1978), and that weed canopy acted in interaction with soil variables (physics, chemistry and microbiology were pooled in this analysis) (Table 5) (Fig. 1a). Teo et *al*. (1989) established that a denser canopy delays the soil dryness and then reduces the soil temperature to the range 5°-25°C, optimal for apothecial stipes development. The soil surface temperature being lowered by evaporation, this temperature reduction would be effective if the soil moisture is high. Therefore, soil physical variables related to higher water retention are more likely to appear conducive for carpogenic germination (Table 3). To the contrary, the DSI was not directly affected by the weed cover (Table 2), which was also illustrated by the slight, non significant, correlation of carpogenic germination with disease severity (Chapter 1) (Fig. 1a), and this contradicted the results of Boland and Hall (1988b) who found significant correlations between the apothecia number and the SSR disease level. However, Boland and Hall (1988b) also noticed that, with the time, the disease aggregation in space progressively decreased compared with the apothecia aggregation due to the ascospores dispersion. As the DSI was measured only one time at the end of the season and, as the weather was very dry during this study, both ascospores dispersion and negative effect of low humidity conditions on ascospores germination might explain the absence of correlation of disease severity with apothecia number. Boland and Hall (1987) also reported the ability of apothecial stipes and apothecia to desiccate and be rehydrated without dying. These results are important for the development of disease risk models

as they point out the necessity to integrate the weather indicators, already used in the models (Workneh and Yang, 2000), with the spatial structure of the active inoculum of *S. sclerotiorum*.

In the sandy loam site (Fig. 6b), the variance explained by 3-y-corn x Urban Compost interaction was entirely shared with soil factors (physico-chemistry and microbiology were pooled in this analysis) (Table 5) and was not spatially structured. This is consistent with the hypothesis that the rotation and fertilization treatments induce suppressiveness through their positive effect on soil health. Rotation, and urban compost fertilization particularly, were associated with higher aggregates stability (MWD) (Tokeshi et *al*., 1997), microbial activity ($PS1_1$, CMQ_1) (Bailey, 1996; Smith, 1972; Sutton and Peng, 1993; Tokeshi et *al*., 1997;) and soil solution concentration (Al_1, CEC_2, P_2) (Singh et *al*., 1995). This analysis also confirmed the conduciveness of fine texture on carpogenic germination in this sandy loam site, as well as the conducive weed effect (Table 3 and 5) (Fig. 1b) (Chapter 2). The fact that the variation explained by the 3-y-corn x Urban Compost interaction was confounded with soil factors only and not shared with canopy or space showed that their effect were independent from their effect on weed canopy, which was not clearly stated in the previous analyses (Chapters 1-2). The explained variation of space and canopy was also low and almost totally shared with soil factors. Then, in the sandy loam site the soil factors largely dominated the SSR variation compared with the clay loam site. However, the pure explained fraction of soil variables was high (35%), but not significant. This supported that soil characteristics affected more directly apothecia, while the effects on DSI were largely spatialized and resulted from the soil physico-chemistry and canopy interaction. This also explained the absence of correlation between disease severity and apothecia number (Fig. 1b) (Chapter 1).

The soil matrix

In the clay loam site (Fig. 7a), the structure of Apothecia-Survival explained variance reflected the general trend shared by the two variables alone, and allowed to precise the effects of factors that influenced these variables. When pooling these two SSR variables, all the pure fractions and sums of pure fractions plus common fractions became significant, except the microbiology one. Thus, the absence of direct link between microbiology noticed for sclerotia survival was probably true for carpogenic germination. The microbiology effect can be explained by a spatially structured variation shared with the soil physico-chemistry and/or canopy factors. The pure spatial variation of Apothecia and sclerotia survival was quite additive. It revealed that the Apothecia spatial pattern was directly linked with the sclerotia survival pattern, which was not surprising but not obvious, as

the sclerotia need to be conditioned (Grau, 1989) before the carpogenic germination to occur. This is consistent with the significant correlation found between apothecia number and sclerotia survival in this clay loam site (Fig. 2a) (Chapter 1). The canopy pure fraction also, rose and became significant when the two SSR variables were pooled. This proves that the canopy, even if it did not affected the survival directly, influenced the conditions of sclerotia germination, and not only the development (and survival) of the apothecial stipes and apothecia. Similarly, the soil physico-chemistry pure fraction became significant along with the sum of the pure and common fractions shared with microbiology, while they were not when computed in the separate analyses. Consequently, in interaction, soil physico-chemistry and microbiology had direct effects on Apothecia-Survival association: their joint effect acted in the same way on both SSR variables as they were additive. Indeed, in the analyses on individual SSR variables, the effects of soil physico-chemistry and microbiology were mostly indirect and acted in interaction with the other factors (space and canopy) (Figs 4a and 5a). The sum of pure and shared fraction of space-physico-chemical factor remained quite the same, as in the separate analyses, supporting the presence of a common spatial pattern of apothecia number and sclerotia survival driven by the soil physico-chemical characteristics (Boland and Hall, 1988b).

In the sandy loam site (Fig. 7b), the pooling of the SSR variables mainly revealed the importance of microbiology, which affected the Apothecia-Survival association directly as revealed by its significant pure fraction (Table 6) (Fig. 2b). Microbiology also acted in interaction with the soil physico-chemical characteristics as shown for Apothecia alone (Fig. 4b). However, the pure physico-chemical fraction was no more significant when the two SSR variables (Apothecia and Survival) are pooled. Indeed, as stated for the regression analysis, the physico-chemistry hardly explained sclerotia survival. Among the microbiology variables, BFI_2 and CMQ_1 were correlated with sclerotia survival which is consistent with the hypothesis of an indirect conducive effect of microbiology on sclerotia survival through its inhibition of carpogenic germination (Mitchell and Wheeler, 1990), as previously stated in the regression analysis on sclerotia survival in this soil.

The case of the Apothecia-Survival association in the sandy loam site was the best illustration of the complex interactions that occur between the soil and *S. sclerotiorum*, and therefore, between all the agrosystem's variables and the SSR disease development. Only the integration of the additive approach (Chapter 2) with the variance partitioning allowed to synthesize the main trends of SSR "ecology" in the two soil sites under study. It also highlighted the importance to study the local

conditions to acquire a global comprehension of the phenomena involved. During the present study, it was tried to introduce a more holistic view of the SSR on soybean development that was made possible, in part, by the development of new statistical tools for experimental ecology (multiple and partial regression/RDA; Borcard et *al*., 1992; Legendre and Legendre, 1998), but also by a more critical approach of the use of classical statistical tools as analysis of variance (Graham and Edwards, 2001; Underwood, 1997). Considering the results of the present study and the increasing interest for a more holistic approach in agronomic problematic, the introduction of numerical ecology in plant pathology may help to adopt a new paradigm for the future of this science: using pathogen agents as indicators of soil and ecosystem health (Hornby and Bateman, 1997) rather than considering them solely as pests. The studies on soil suppressiveness have accumulated evidences that, even if the more ecological cultural practices as soil conservation practices or organic fertilization do not necessarily suppress all the diseases, they don't induce an enhancement of the disease incidence (Bailey and Lazarovits, 2003), but always contribute to reduce the impacts of intensive agriculture on the ecosystems.

Acknowledgements

The author acknowledges the Conseil des recherches en pêche et en agroalimentaire du Québec (CORPAQ) and the Fédération des producteurs de cultures commerciales du Québec (FPCCQ) financial support for this study. The author gratefully acknowledges Drs. Daniel Borcard and Pierre Legendre for their precious help and skillful assistance in the multivariate analyses. The author is also grateful to Roselyne Labbé for reviewing this chapter.

Table 1. Sclerotinia stem rot variables, rotation and fertilization treatments, environmental variables (plant canopy, weeds and soil), and methods of analysis used in the clay loam and sandy loam sites, in Saint-Hyacinthe, 2002.

Variables	Unit	Abbreviation	Method/reference
***Sclerotinia* stem rot**			
Disease severity index	%	DSI	Grau and Radke (1984)
Carpogenic germination	# m^{-2}	Apothecia	-
Sclerotia survival	%	Survival	-
Treatments			
Corn-corn-corn-soybean	-	3-y-corn	-
Corn-corn-soybean-soybean	-	2-y-corn	-
Soybean-soybean-soybean-soybean	-	4-y-Monoculture	-
Mineral fertilization	-	NPK	-
Urban compost fertilization	-	Urban Compost	-
Canopy			
Soybean phenology			
Leaf area index at stage R2-R3	-	LAI1	LI-Cor ®
Leaf area index at stage R5-R6	-	LAI2	LI-Cor ®
Soybean yield	$kgHa^{-1}$	Yield	-
Weed biomass			
Amaranthus retroflexus	$kgHa^{-1}$	*Ama. ret.*	-
Chenopodium album	"	*Che. alb.*	-
Ambrosia artemisiifolia	"	*Amb. art.*	-
Brassica kaber	"	*Bra. kab.*	-
Polygonum aviculare	"	*Pol. avi.*	-
Dicotyledon	"	Tdicot.	-
Monocotyledon	"	Tmonocot.	-
Total biomass	"	Tweeds	-
Soil			
Physics			
Clay	%	Clay	Gee and Bauder (1986)
Silt	"	Silt	"
Sand	"	Sand	"
Mean weight diameter	mm	MWD	Kemper and Rosenau (1986)
Organic matter	%	OM	CPVQ 1988
Field capacity	"	FC	Cassel and Nielsen (1986)
Chemistry			
pH	-	pH	
Cation exchance capacity	meqL-1	CEC	AFEQ, 1990
Total carbon	%	C	LECO CNS 2000 ®
Total nitrogen	"	N	"
Carbon : nitrogen ratio	-	C/N	-
Total sulphur	%	S	LECO CNS 2000 ®
Phosphorus	ppm	P	Mehlich III
Potassium	"	K	"
Calcium	"	Ca	"
Magnesium	"	Mg	"
Aluminium	"	Al	"
Microbiology			
Carbon mineralization quotient	-	CMQ	Rousseau and Schaefer (2003)
Direct counts in physiologic saline solution	10^6 cells mL^{-1}	PS1	Rusch (1972)
Direct counts in physiologic saline solution + 5 gL^{-1} Lactose and 5 gL^{-1} Dextrose	"	PS2	"
Biological fertility index	4 groups	BFI	"

Table 2: Disease severity (DSI) variance explained by spatial and environmental variables retained after forward selection in the multiple regression based on each set of environmental variables (independent selection), in the clay loam and sandy loam sites, in 2002.

	Clay loam				Sandy loam			
Variable set	***Variable*[z]**	**Explained variance (%)**	**r**	***P*-value**	***Variable***	**Explained variance (%)**	**r**	***P*-value**
Spatial[w]	***none***				x^2y^3	21	-0.46	0.036
					xy^2	13	0.36	0.065
					x	18	0.02	0.018
					Model	51.6	0.72	0.005
Treatments[v]	***Rot1***	25	-0.52	0.05	***Rot*Fert1***	14.8	-0.67	0.018
	Rot2	11	-0.34	0.11				
	Model	36.4	0.62	0.05				
Canopy	***Yield***	51	-0.71	0.001	***Tweeds***	24	0.49	0.013
	LAI1	10	0.01	0.025	***Ama. ret.***	11	0.28	0.072
	Model	61.4	0.78	0.001	***Model***	35.2	0.59	0.013
Physics	***Silt2***	13	-0.36	0.091	OM_2	21.3	0.46	0.023
	OM_1	8	0.26	0.14				
	OM_2	12	-0.004	0.074				
	MWD	13	-0.02	0.045				
	Model	46.5	0.68	0.009				
Chemistry	S_2	18	-0.43	0.039	C_1	20	0.45	0.028
	CN_1	10	-0.27	0.094	P_2	15	0.45	0.036
					CEC_2	14	-0.13	0.022
	Model	28.3	0.53	0.031	***Model***	49.4	0.7	0.002
Microbiology	$PS1_1$	16	0.40	0.049	***none***			
	$PS1_2$	13	0.19	0.059				
	Model	29.1	0.54	0.024				

[z] The soil variables were labeled $_1$ or $_2$ if they were measured in 0-10 cm soil depht (A_1) or in 10-20 cm soil depht (A_2)
[w] Spatial variables x^2y^3, xy^2, x were terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)
[v] treatments were coded by dummy variables: Rot1, Rot2 for rotation; Fert for fertilization; Rot*Fert1, Rot*Fert2 for the interactions (Legendre and Anderson, 1999)
See Table 1 for the abbreviations.

Table 3: Carpogenic germination (Apothecia) variance explained by spatial and environmental variables retained after forward selection in the multiple regression based on each set of environmental variables (independent selection), in the clay loam and sandy loam sites, in 2002.

	Clay loam				Sandy loam			
Variable set	***Variable*** [z]	**Explained variance (%)**	**r**	***P*-value**	***Variable***	**Explained variance (%)**	**r**	***P*-value**
Spatial[w]	x^2y^2	37	0.61	0.006	y^3	26.0	-0.51	0.009
	x^2y^3	34	0.59	0.001				
	xy	13	-0.36	0.001				
	Model	84.2	0.92	0.001				
Canopy	***Tdicot***	37	0.61	0.007	***Art. amb.***	32.0	0.57	0.011
	Pol. avi.	15	0.24	0.026				
	Model	51.9	0.72	0.012				
Physics[v]	***MWD***	13	0.36	0.074	$Clay_1$	35	0.59	0.005
	$Sand_1$	12	0.17	0.075	***MWD***	18	-0.23	0.013
	CS_2	13	0.29	0.075				
	SCL_1	11	0.05	0.042				
	Model	48.9	0.7	0.018	***Model***	52.8	0.73	0.002
Chemistry	P_2	37	-0.61	0.007	Al_1	29	-0.54	0.006
	Al_2	12	-0.04	0.043	S_2	11	0.15	0.092
	Ca_1	7	0.26	0.068	Al_2	10	-0.49	0.055
	K_1	6	0.07	0.093				
	C_1	8	0.31	0.036				
	Model	70.2	0.84	0.002	***Model***	50.4	0.71	0.007
Microbiology	$PS1_1$	22.0	0.47	0.037	$PS1_1$	17	-0.41	0.052
					CMQ_1	14	-0.33	0.064
					BFI_2	10	-0.3	0.064
					Model	40.8	0.64	0.016

[z] The soil variables were labeled $_1$ or $_2$ if they were measured in 0-10 cm soil depht (A_1) or in 10-20 cm soil depht (A_2)

[w] Spatial variables x^2y^2, x^2y^3, xy, y^3 were terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)

[v] CS: clay soil; SCL: sand-clay loam

See Table 1 for the abbreviations.

Table 4: Sclerotia survival (Survival) variance explained by spatial and environmental variables retained after forward selection in the multiple regression based on each set of environmental variables (independent selection), in the clay loam and sandy loam sites, in 2002.

		Clay loam				Sandy loam		
Variable set	***Variable*** [z]	**Explained variance (%)**	**r**	***P*-value**	***Variable***	**Explained variance (%)**	**r**	***P*-value**
Spatial [w]	x^2y^2	41	0.64	0.002	***none***			
	x^2y^3	27	0.52	0.002				
	x^3y	5	-0.22	0.077				
	Model	72.8	0.85	0.001				
Canopy	***Pol. avi.***	19	0.43	0.042	***none***			
	Tdicot.	14	0.27	0.045				
	Model	33.2	0.58	0.028				
Physics	***MWD***	19	0.44	0.029	***none***			
	$Sand_1$	36	0.36	0.001				
	$Clay_2$	14	0.07	0.009				
	Model	69.0	0.83	0.001				
Chemistry	N_2	40	-0.63	0.002	pH_1	15	0.38	0.071
	P_2	11	-0.57	0.001	P_1	15	0.31	0.041
	Model	51.2	0.72	0.001	***Model***	30.0	0.55	0.032
Microbiology	$PS1_2$	22.5	0.47	0.011	BFI_1	19.9	0.45	0.024

[z] The soil variables were labeled $_1$ or $_2$ if they were measured in 0-10 cm soil depht (A_1) or in 10-20 cm soil depht (A_2)

[w] Spatial variables x^2y^2, x^2y^3, x^3y were terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)

See Table 1 for the abbreviations.

Table 5: Disease severity (DSI) and carpogenic germination (Apothecia) (aerial matrix) variance explained by spatial and environmental variables retained after forward selection in the RDA based on each set of environmental variables (independent selection), in the clay loam and sandy loam sites, in 2002.

	Clay loam					Sandy loam				
Variable set	***Variable*** [z]	**Explained variance (%)**	**Canonical coefficients**		***P*-value**	***Variable***	**Explained variance (%)**	**Canonical coefficients**		***P*-value**
			RDA I	**RDA II**				**RDA I**	**RDA II**	
Spatial[w]	x^2y^2	21	0.57	0.04	0.011	y^3	19.3	-0.57	0	0.01
	x^2y^3	21	0.57	0.02	0.006					
	xy	7	-0.29	-0.19	0.097					
	x^3y	8	-0.32	-0.03	0.052					
	Model	56.7	0.87	0.47	0.001					
	Eigenvalues		0.49	0.08						
Treatments[v]	***Rot1***	16	0.53	0.12	0.036	***Rot*Fert1***	8	-0.6	0	0.055
Canopy	***Tdicot***	41	0.78	0.02	0.001	***Art. amb.***	24.2	0.64	0	0.006
	Pol. avi.	9	0.14	-0.21	0.041					
	Yield	6	-0.67	-0.27	0.085					
	Model	55.9	0.86	0.43	0.001					
	Eigenvalues		0.5	0.06						
Physics[u]	$Silt_2$	8	-0.33	0.16	0.142	$Clay_1$	18	0.55	-0.14	0.012
	OM_1	9	0.32	0	0.117	***MWD***	14	-0.29	-0.13	0.026
	OM_2	17	-0.07	-0.09	0.01	SL_2	8	0.15	-0.41	0.072
	Model	33.9	0.69	0.2	0.005	***Model***	39.7	0.73	0.46	0.001
	Eigenvalues		0.33	0.01		***Eigenvalues***		0.31	0.09	
Chemistry	P_2	19	-0.43	-0.42	0.02	Al_1	21	0.58	0.13	0.006
	Al_1	11	-0.49	0.1	0.056	S_2	8	-0.37	0.23	0.097
	S_2	6	0.35	-0.3	0.147	P_2	7	0.55	-0.05	0.107
	CEC_1	11	-0.26	0.22	0.04	CEC_2	12	0.09	0.3	0.025
	Model	47.0	0.71	0.63	0.005	***Model***	48.3	0.75	0.59	0.001
	Eigenvalues		0.34	0.13		***Eigenvalues***		0.34	0.14	
Microbiology	$PS1_1$	18.8	0.53	0	0.024	$PS1_1$	16	-0.49	-0.19	0.026
						CMQ_1	10	-0.17	0.45	0.053
						Model	26.1	0.54	0.47	0.007
						Eigenvalues		0.17	0.09	

[z] The soil variables were labeled $_1$ or $_2$ if they were measured in 0-10 cm soil depht (A_1) or in 10-20 cm soil depht (A_2)

[w] Spatial variables x^2y^2, x^2y^3, xy, x^3y, y^3 were terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)

[v] treatments were coded by dummy variables: Rot1, Rot2 for rotation; Fert for fertilization; Rot*Fert1, Rot*Fert2 for the interactions (Legendre and Anderson, 1999)

[u] SL: sandy loam

See Table 1 for the abbreviations.

Table 6: Carpogenic germination (Apothecia) and sclerotia survival (Survival) (soil matrix) variance explained by spatial and environmental variables retained after forward selection in the RDA based on each set of environmental variables (independent selection), in the clay loam and sandy loam sites, in 2002.

Variable set	Clay loam					Sandy loam				
	Variable[z]	Explained variance (%)	Canonical coefficients		*P*-value	*Variable*	Explained variance (%)	Canonical coefficients		*P*-value
			RDA I	RDA II				RDA I	RDA II	
Spatial[w]	x^2y^2	39	0.67	0.09	0.002	y^3	12.8	-0.5	0	0.05
	x^2y^3	30	0.6	-0.04	0.001					
	x^3y	9	-0.31	0.13	0.002					
	Model	77.8	0.95	0.16	0.001					
	Eigenvalues		0.77	0.01						
Canopy	***Tweeds***	22	0.5	-0.2	0.017	***Art. amb.***	23.8	0.67	0	0.004
	Pol. avi.	21	0.35	0.35	0.011					
	Model	42.6	0.69	0.41	0.011					
	Eigenvalues		0.4	0.03						
Physics[v]	CL_2	17	-0.45	-0.11	0.01	$Clay_1$	20.8	0.65	0	0.006
	$Clay_1$	12	-0.25	0.12	0.053					
	MWD	14	0.44	0.06	0.031					
	Model	42.9	0.71	0.15	0.013					
	Eigenvalues		0.42	0.01						
Chemistry	P_2	35	-0.64	0.09	0.003	Al_1	14	0.53	0.04	0.032
	N_2	11	-0.57	-0.25	0.034	Ca_1	10	-0.14	0.35	0.089
	Al_2	6	-0.01	0.02	0.093	CN_1	8	0.11	-0.03	0.098
	Model	52.4	0.77	0.37	0.002	P_2	8	0.38	0.23	0.093
	Eigenvalues		0.5	0.02		S_2	9	-0.12	-0.06	0.082
						Al_2	7	0.47	0.19	0.088
						CEC_2	7	0.26	-0.11	0.085
						Model	62.8	0.81	0.77	0.003
						Eigenvalues		0.33	0.29	
Microbiology	$PS1_2$	22.0	0.51	0	0.007	CMQ_1	14	0.54	0.09	0.026
						$PS1_1$	14	-0.07	0.5	0.024
						$PS2_1$	10	0.05	0.34	0.031
						BFI_2	9	0.46	0.1	0.066
						Model	47.0	0.74	0.63	0.001
						Eigenvalues		0.26	0.21	

[z] The soil variables were labeled $_1$ or $_2$ if they were measured in 0-10 cm soil depht (A_1) or in 10-20 cm soil depht (A_2)

[w] Spatial variables x^2y^2, x^2y^3, x^3y, y^3 were terms of cubic trend surface regression of plot coordinates selected by forward selection procedure of CANOCO 4.5 (ter Braak and Smilauer, 2002; Borcard et *al*., 1992)

[v] CL: clay loam.

See Table 1 for the abbreviations

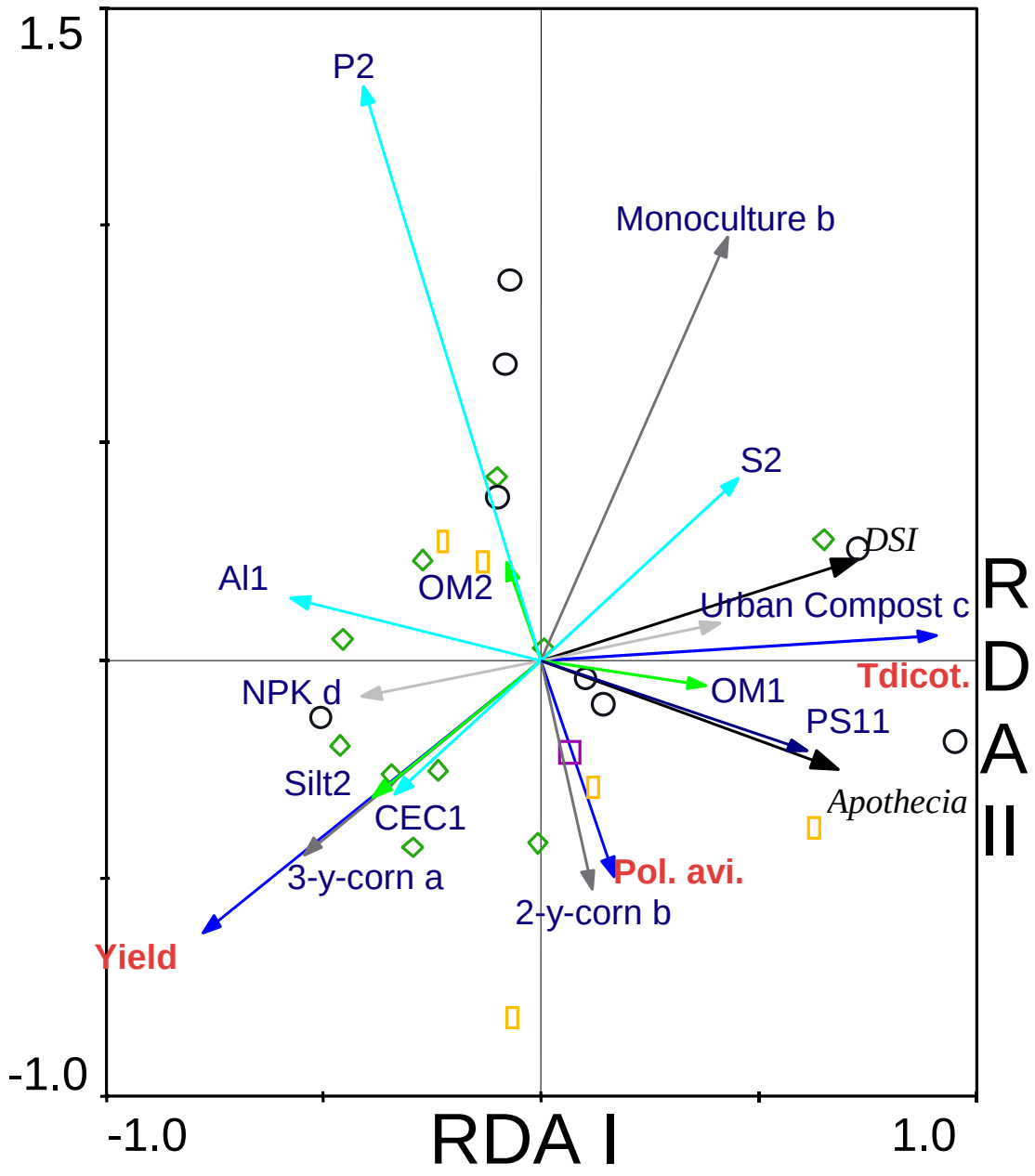

Figure 1a. Clay loam, 2002: redundancy analysis (RDA) correlations triplot of disease severity (*DSI*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by independent forward selection, and treatments (rotation and fertilization). Abbreviations are given in Table 1. The soil physico-chemistry variables and the treatments are included as passive variables in the analysis. Treatments with same letters indicate no significant difference ($P > 0.05$. The RDA axis I displays 50% and axis II 6% of the DSI-Apothecia matrix with canopy variables as active variables (Table 5). Samples are classified by soil type: ○ Sand-clay loam; ▯ Sand-clay soil; ◊ Clay loam; □ Clay soil.

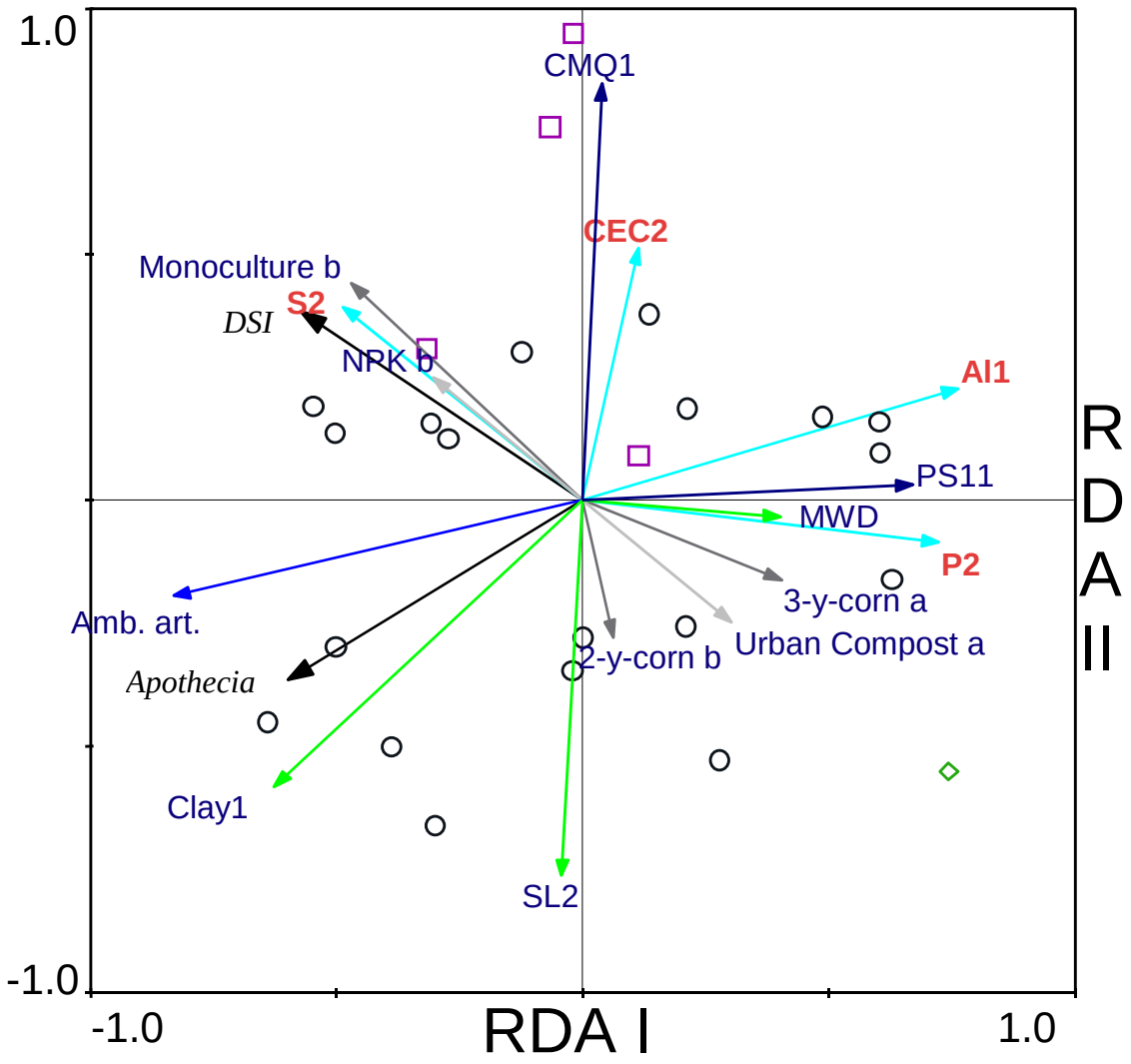

Figure 1b. Sandy loam, 2002: redundancy analysis (RDA) correlations triplot of disease severity (*DSI*) and carpogenic germination (*Apothecia*) with environmental variables, as selected by independent forward selection, and treatments (rotation and fertilization). Abbreviations are given in Table 1 (SL: sandy loam). The canopy, soil physics and microbiology variables, and the treatments are included as passive variables in the analysis. Treatments with same letters indicate no significant difference ($P > 0.05$). The RDA axis I displays 34% and axis II 14% of the DSI-Apothecia matrix with chemistry variables as active variables (Table 5). Samples are classified by soil type: ○ Sandy loam; □ Loamy sand; ◊ Sand-clay soil.

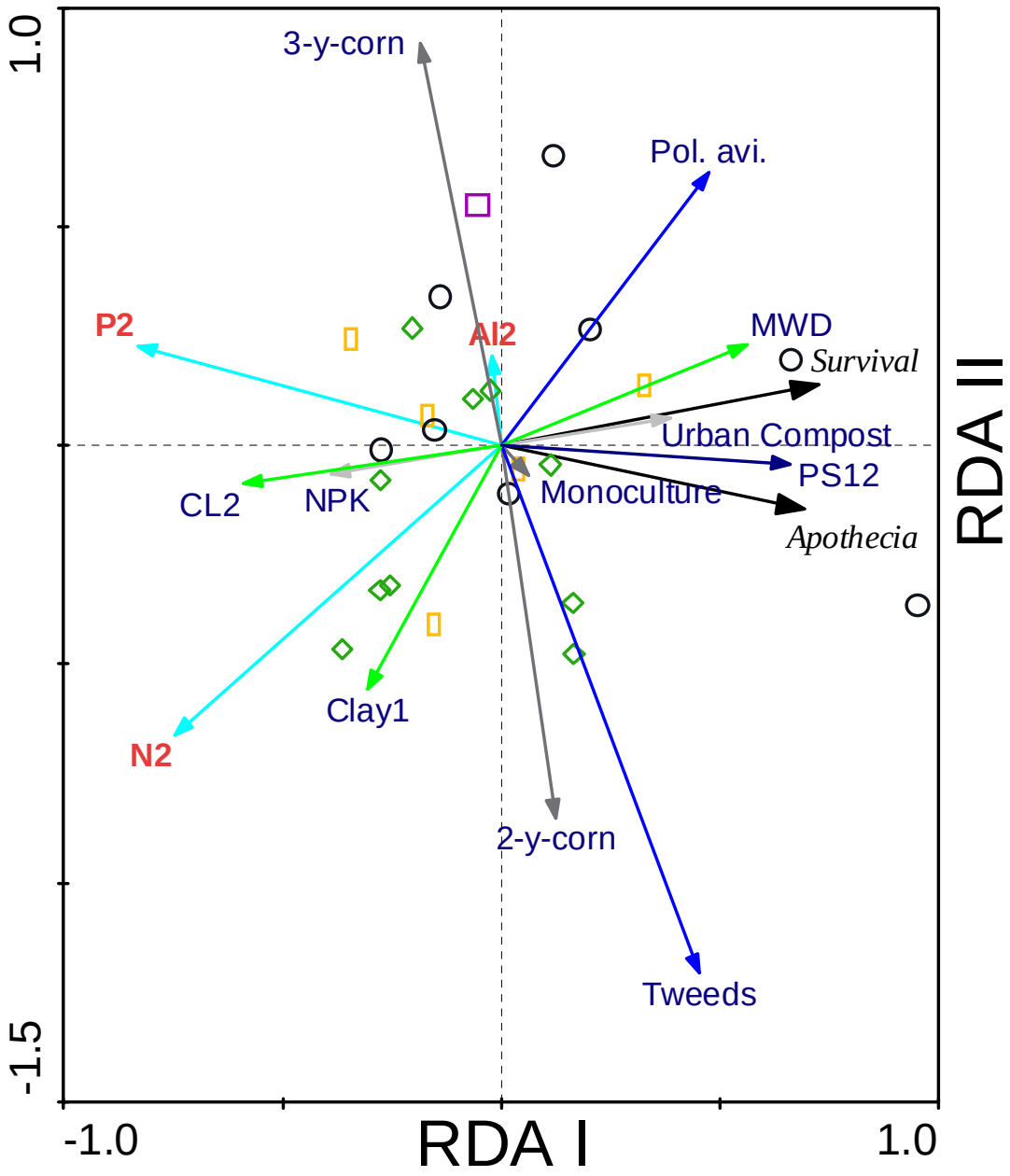

Figure 2a. Clay loam, 2002: redundancy analysis (RDA) correlations triplot of carpogenic germination (*Apothecia*) and sclerotia survival (*Survival*) with environmental variables, as selected by independent forward selection, and treatments (rotation and fertilization). Abbreviations are given in Table 1 (CL: clay loam). The canopy, soil physics and microbiology variables, and the treatments are included as passive variables in the analysis. The RDA axis I displays 50% and axis II 2% of the Apothecia-Survival matrix with chemistry variables as active variables (Table 6). Samples are classified by soil type: ○ Sand-clay loam; ▯ Sand-clay soil; ◊ Clay loam; □ Clay soil.

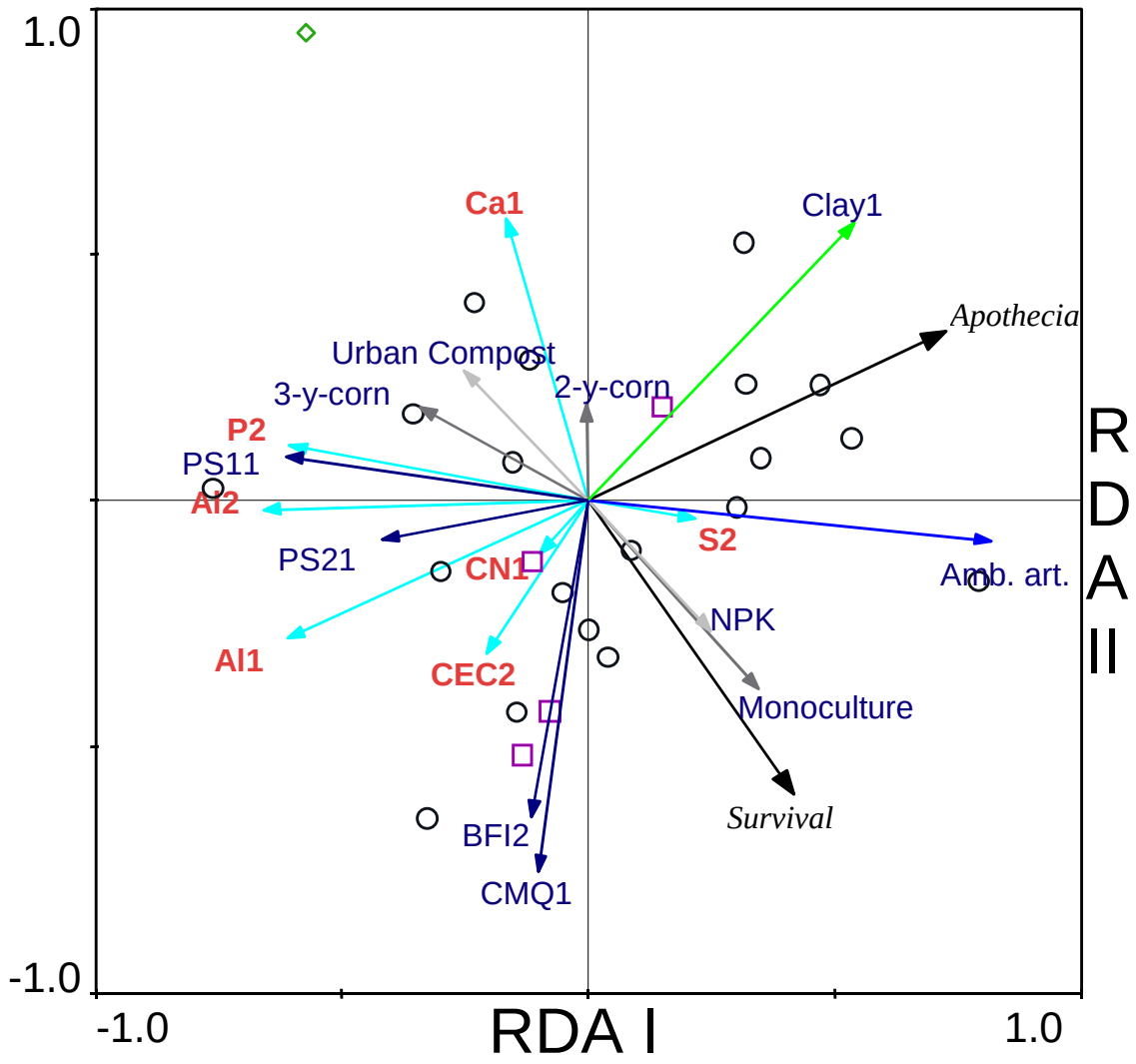

Figure 2b. Sandy loam, 2002: redundancy analysis (RDA) correlations triplot of carpogenic germination (*Apothecia*) and sclerotia survival (*Survival*) with environmental variables, as selected by independent forward selection, and treatments (rotation and fertilization). Abbreviations are given in Table 1. The canopy, soil physics and microbiology variables, and the treatments are included as passive variables in the analysis. The RDA axis I displays 33% and axis II 29% of the Apothecia-Survival matrix with chemistry variables as active variables (Table 6). Samples are classified by soil type: ○ Sandy loam; □ Loamy sand; ◊ Sand-clay soil.

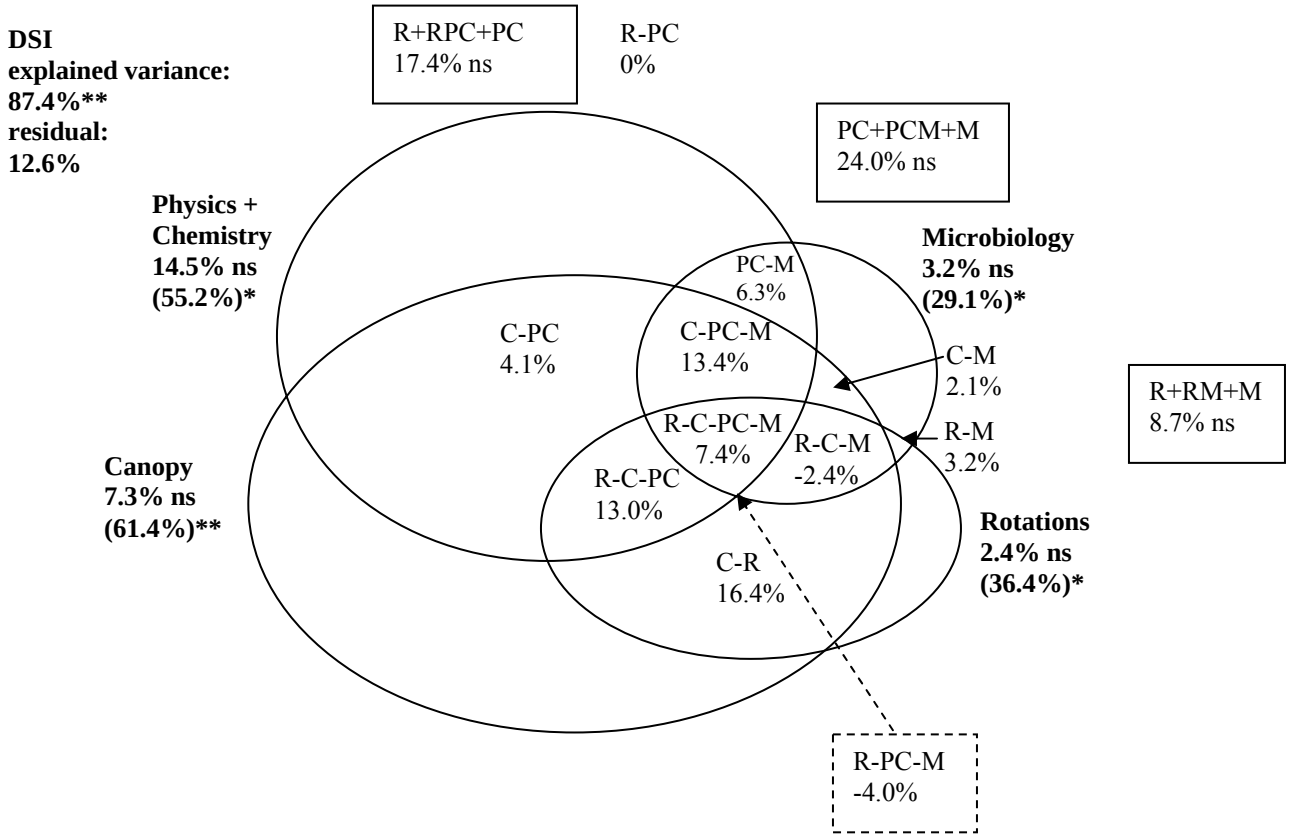

Figure 3a. Clay loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of disease severity variance (DSI) by four tables of explanatory variables: rotations (R), canopy (C), soil physico-chemical characteristics (physics + chemistry = PC), and soil microbiological activity (microbiology = M). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant). Fraction framed by dashed line cannot be represented in two dimensions.

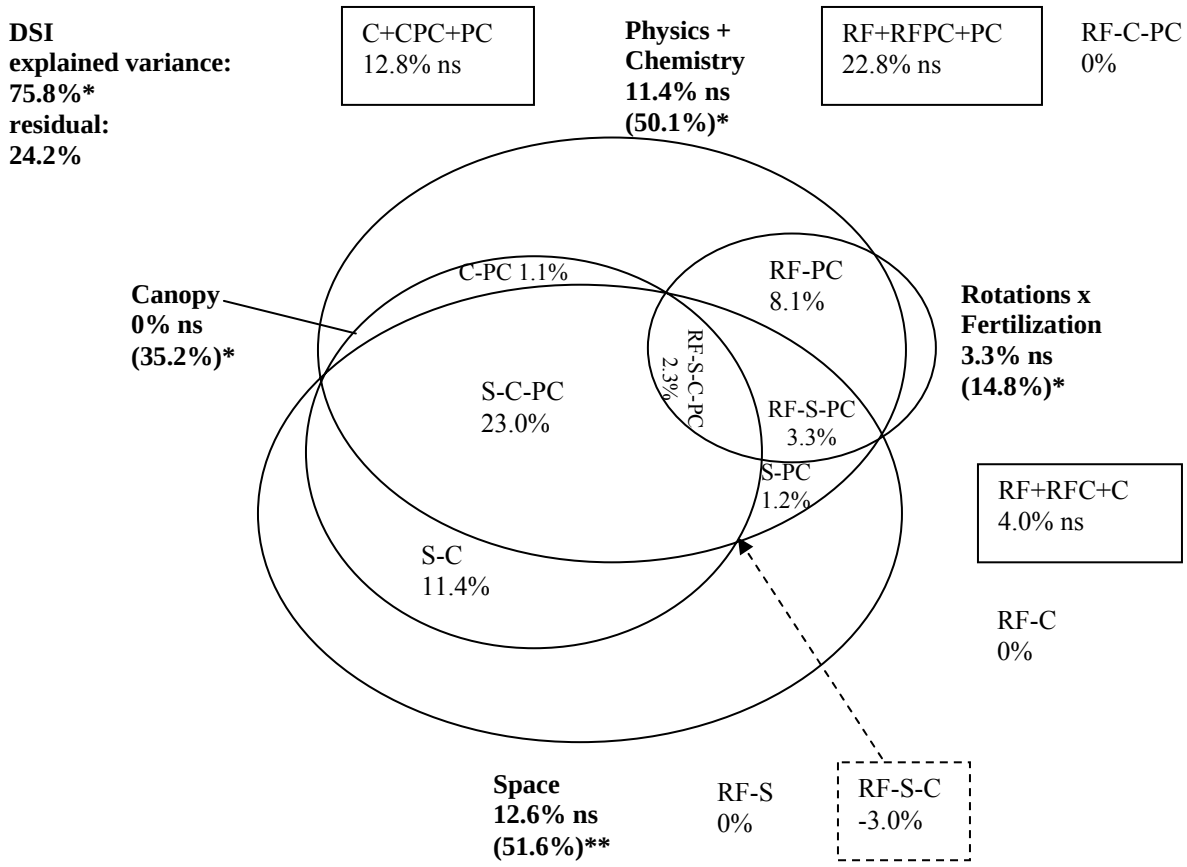

Figure 3b. Sandy loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of disease severity variance (DSI) by four tables of explanatory variables: interaction rotation x fertilization (RF), space (S), canopy (C), and soil physico-chemical characteristics (physics + chemistry = PC). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant). Fraction framed by dashed line cannot be represented in two dimensions.

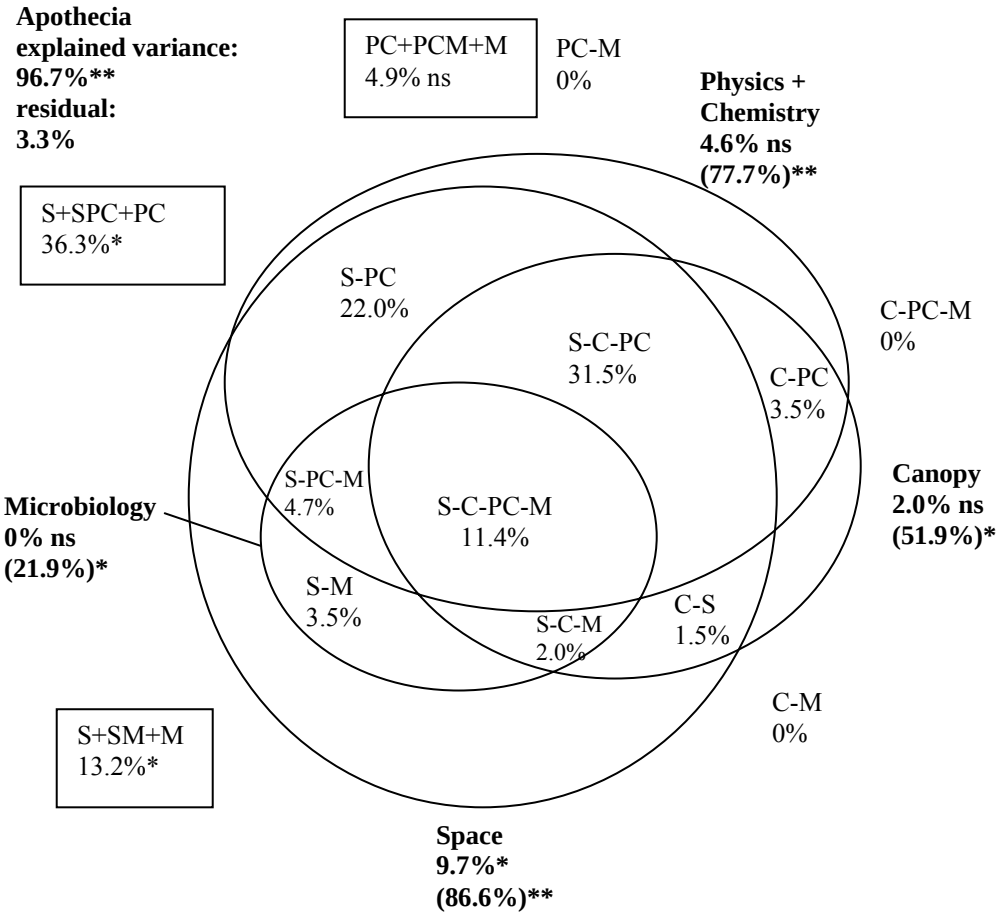

Figure 4a. Clay loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of carpogenic germination variance (Apothecia) by four tables of explanatory variables: space (S), canopy (C), soil physico-chemical characteristics (physics + chemistry = PC), and soil microbiological activity (microbiology = M). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant).

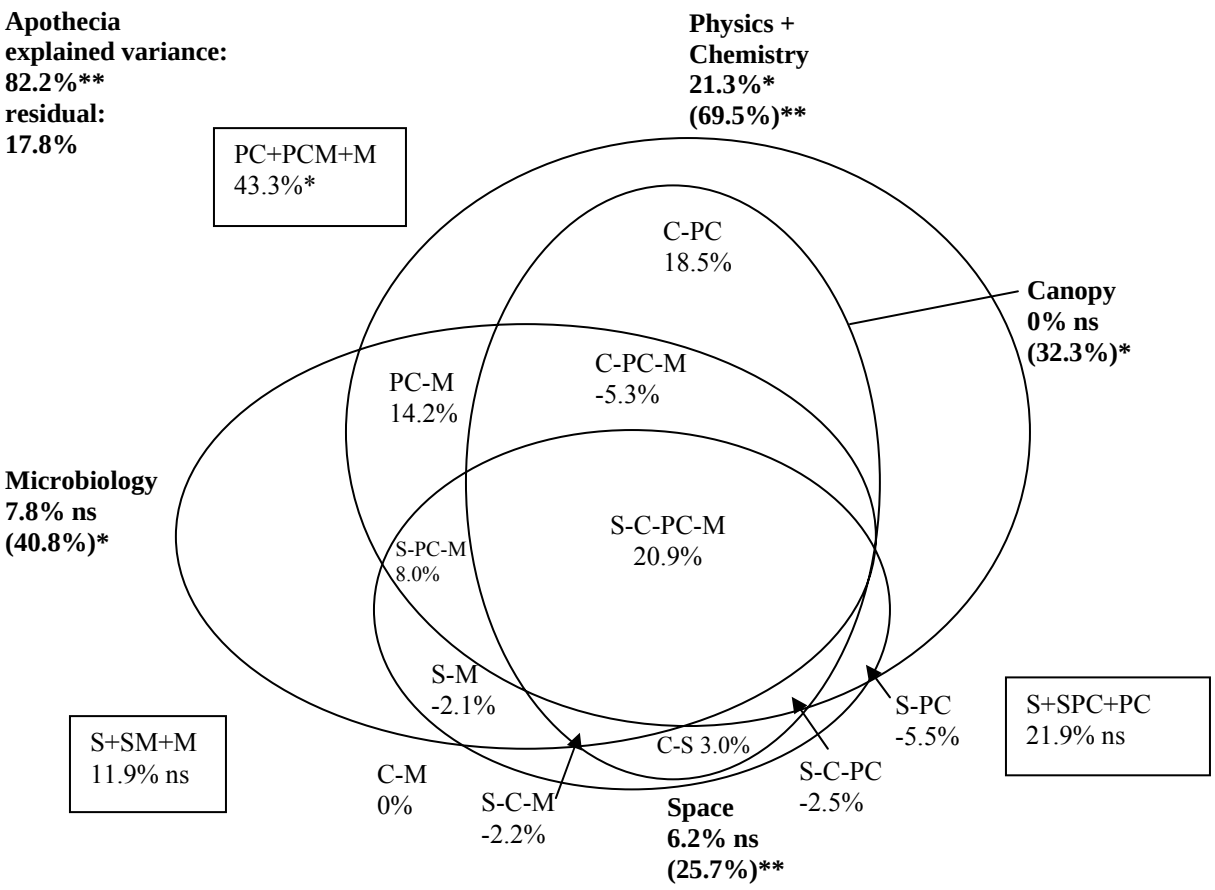

Figure 4b. Sandy loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of carpogenic germination variance (Apothecia) by four tables of explanatory variables: space (S), canopy (C), soil physico-chemical characteristics (physics + chemistry = PC), and soil microbiological activity (microbiology = M). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant).

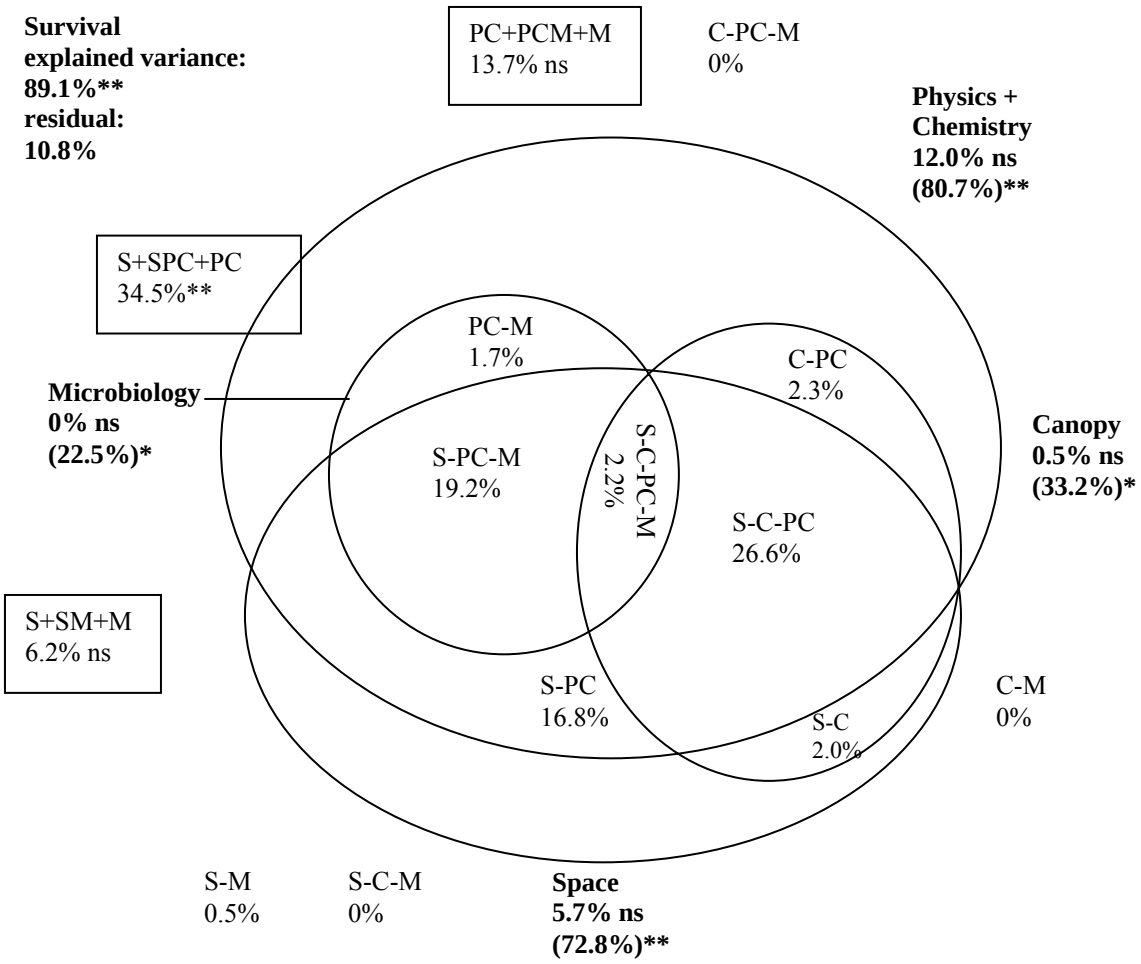

Figure 5a. Clay loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of sclerotia survival variance (Survival) by four tables of explanatory variables: space (S), canopy (C), soil physico-chemical characteristics (physics + chemistry = PC), and soil microbiological activity (microbiology = M). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant).

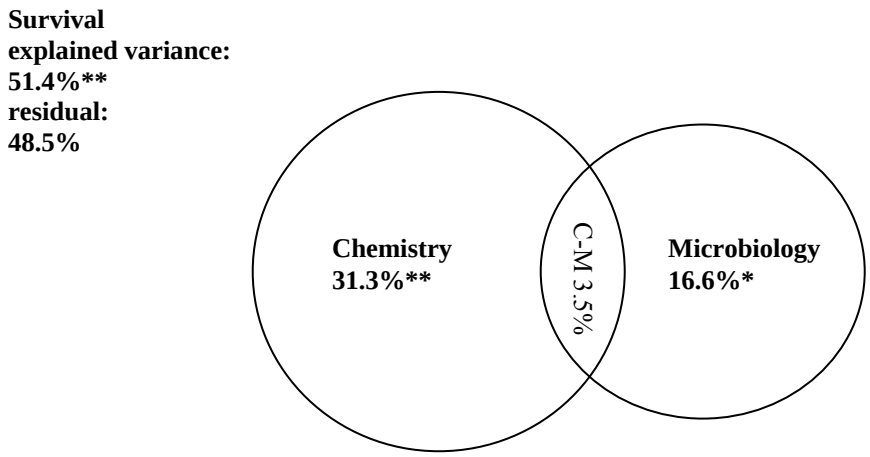

Figure 5b. Sandy loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of sclerotia survival variance (Survival) by two tables of explanatory variables: soil chemical characteristics (chemistry = C) and soil microbiological activity (microbiology = M). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant).

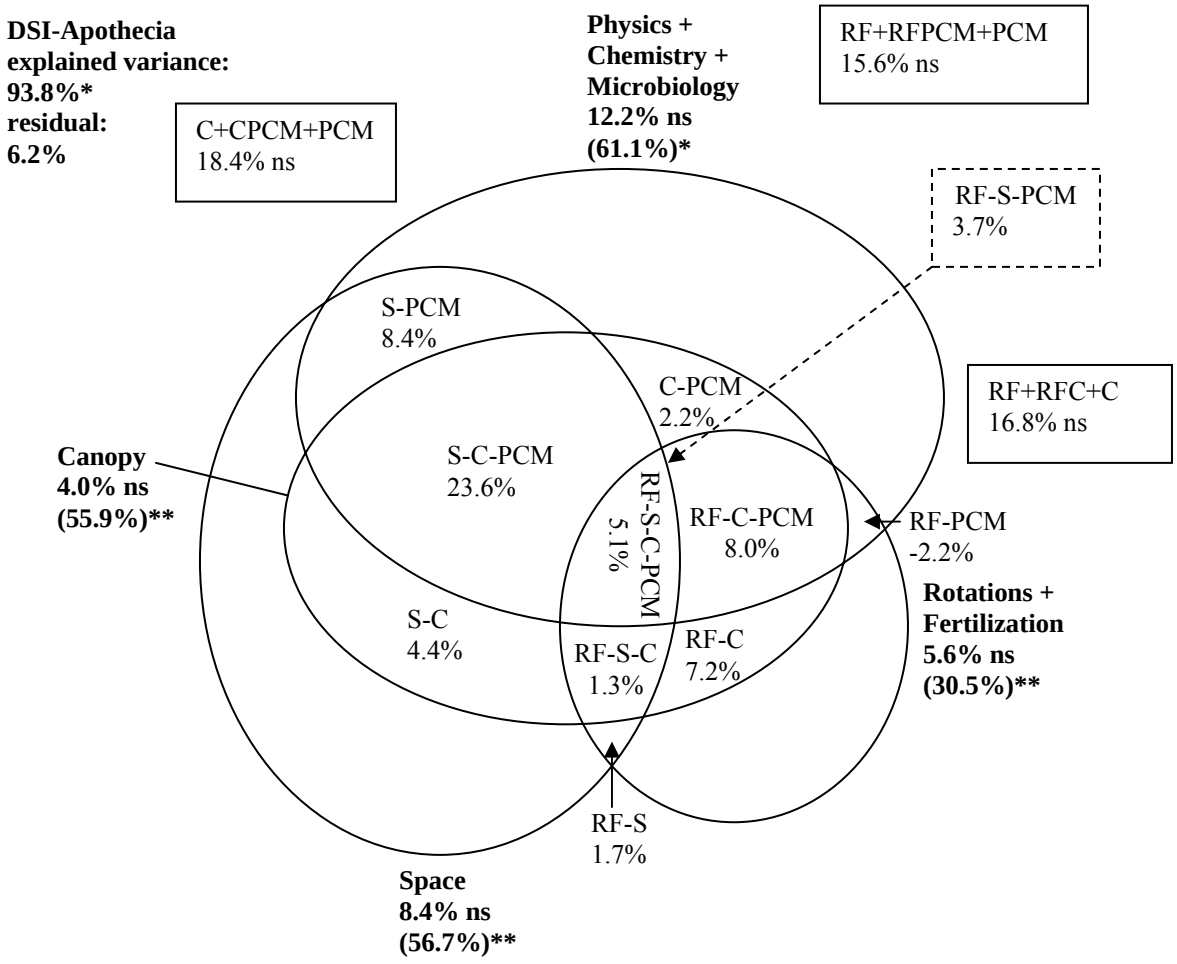

Figure 6a. Clay loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of disease severity and carpogenic germination variance (DSI-Apothecia) by four tables of explanatory variables: rotation and fertilization (RF), space (S), canopy (C), soil physico-chemical, and microbiological characteristics (physics + chemistry + microbiology = PCM). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant). Fraction framed by dashed line cannot be represented in two dimensions.

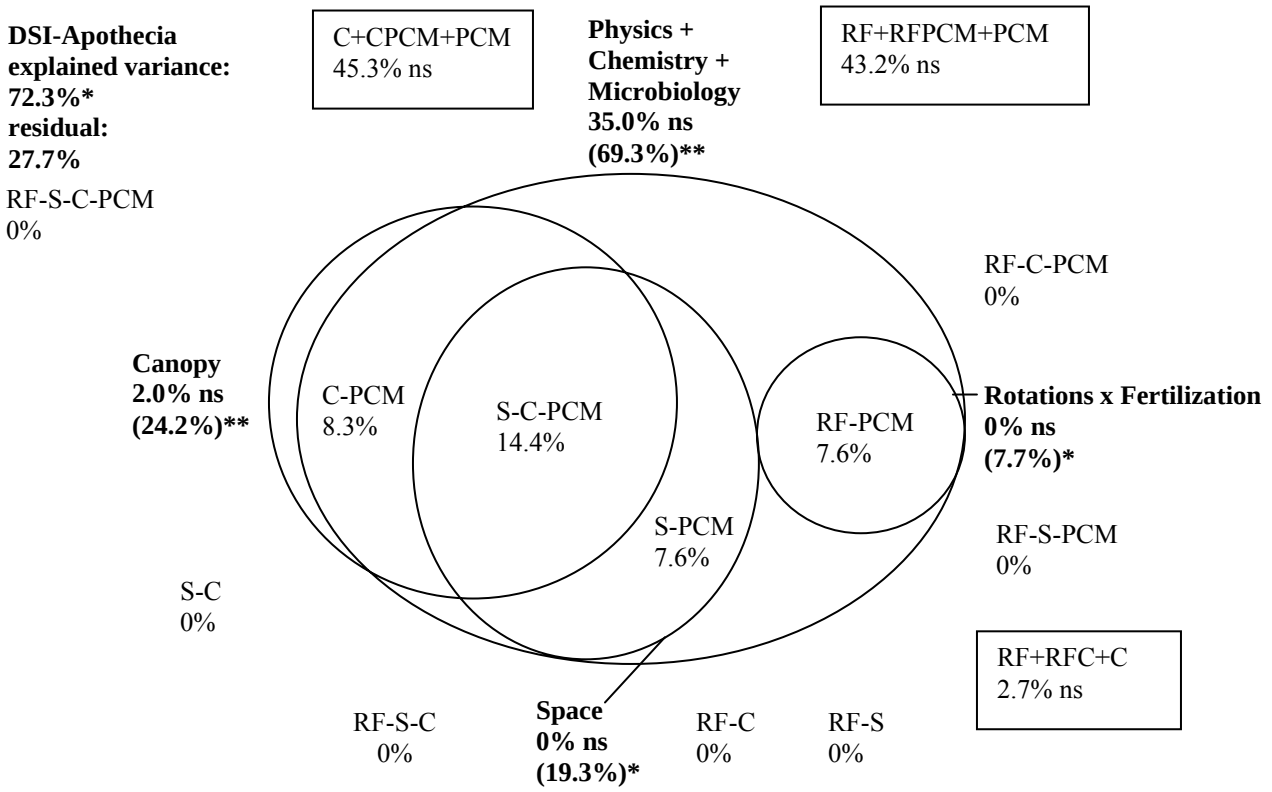

Figure 6b. Sandy loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of disease severity and carpogenic germination variance (DSI-Apothecia) by four tables of explanatory variables: interaction rotation x fertilization (RF), space (S), canopy (C), soil physico-chemical, and microbiological characteristics (physics + chemistry + microbiology = PCM). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant).

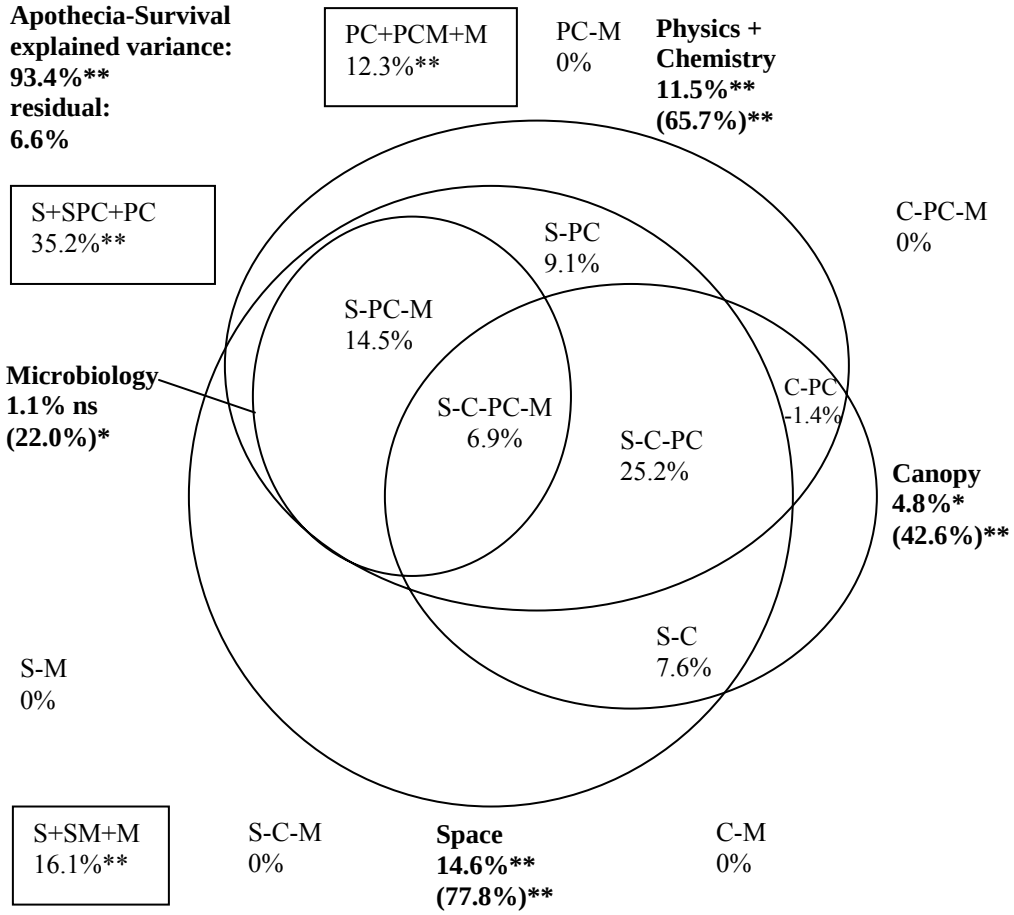

Figure 7a. Clay loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of carpogenic germination and sclerotia survival variance (Apothecia-Survival) by four tables of explanatory variables: space (S), canopy (C), soil physico-chemical characteristics (physics + chemistry = PC), and soil microbiological activity (microbiology = M). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant).

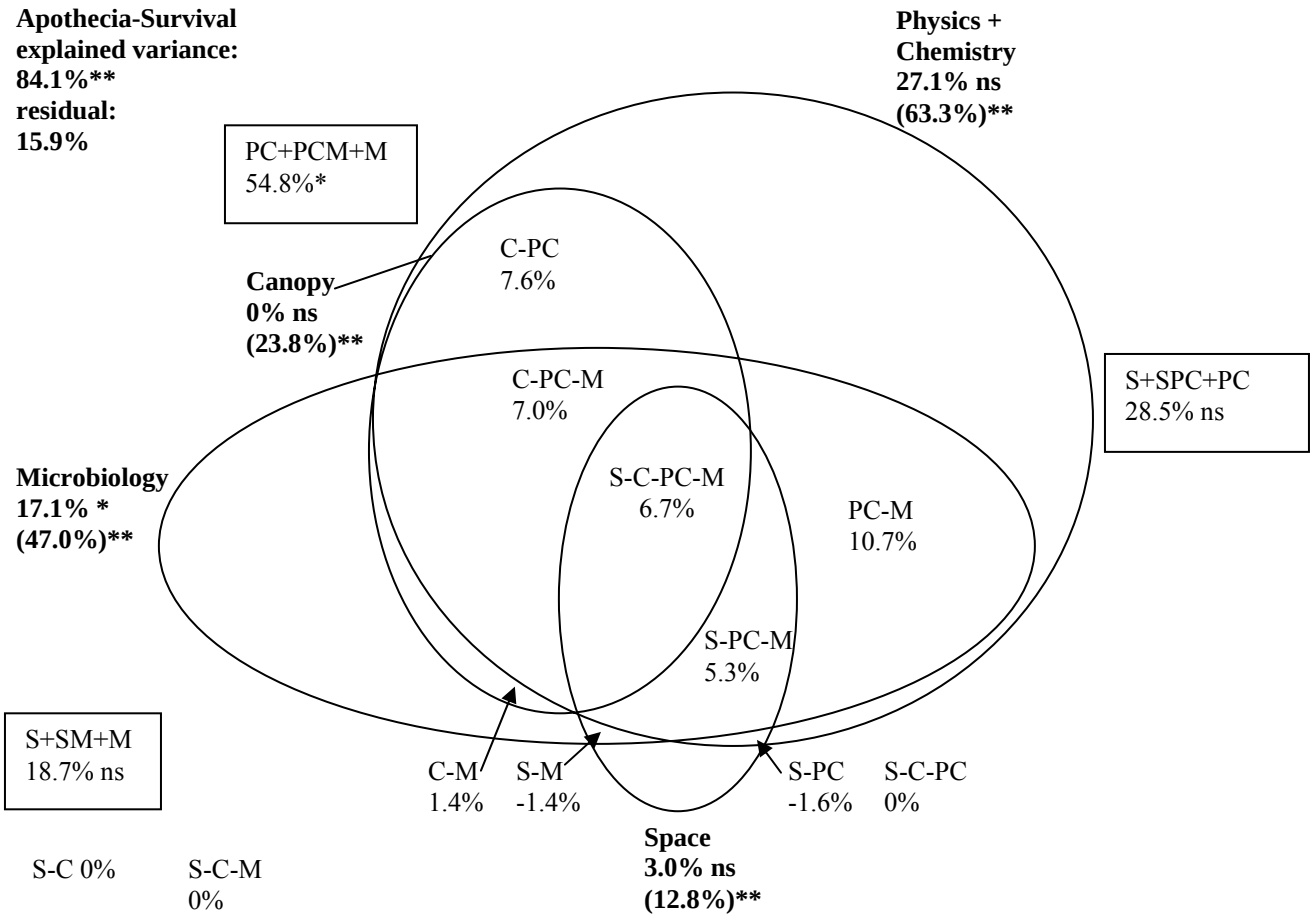

Figure 7b. Sandy loam, 2002: diagram showing the marginal and conditional fractions for the partitioning of carpogenic germination and sclerotia survival variance (Apothecia-Survival) by four tables of explanatory variables: space (S), canopy (C), soil physico-chemical characteristics (physics + chemistry = PC), and soil microbiological activity (microbiology = M). Percentage of explained variation and results of permutation tests (999 permutations) are indicated for testable fractions (* $P < 0.05$ and ** $P < 0.01$; ns = non significant).

DISCUSSION GÉNÉRALE

Dans cette thèse, on a étudié les effets de l'amendement avec un compost urbain, comparé à la fertilisation minérale, ainsi que les effets de la rotation avec le maïs, comparée à la monoculture du soja, sur le développement de la sclérotiniose du soja dans un loam argileux et un loam sableux. On s'intéressait en particulier aux caractéristiques du sol et du couvert végétal, à leur réponse aux traitements de rotation et de fertilisation et à leurs relations avec la santé du sol et l'écologie de la sclérotiniose.

Dans le chapitre 1, des effets distincts des traitements rotation et fertilisation ont été mis en évidence entre les deux sites. Au site argileux, la rotation de 3 ans avec le maïs diminuait significativement la gravité de la sclérotiniose du soja, tandis que l'apport de MO sous forme de compost urbain contribuait à l'augmenter. Au site sableux, l'action combinée du compost urbain et de la rotation de 3 ans avec le maïs a entraîné une réduction significative de la gravité de la maladie. Ces résultats appuient le potentiel suppressif de la rotation et, dans une moindre mesure, celui du compost urbain et mettent en évidence l'effet du type de sol comme facteur déterminant de l'effet de la rotation et du compost urbain sur la sclérotiniose.

L'utilisation de la régression multiple a permis notamment d'estimer la contribution relative de chacun des traitements sur les variables de sclérotiniose, ce qui constitue une composante essentielle de l'ANOVA en écologie, composante encore très souvent négligée (Graham et Edwards, 2001). L'analyse canonique des redondances (ACR) sur les corrélations entre les variables de la sclérotiniose a notamment contribué à préciser l'effet des traitements sur la production d'apothécies et la survie des sclérotes par rapport à l'ANOVA. En effet, au site argileux, l'ACR suggère que le compost urbain favorise la levée ou la survie des stipes et des apothécies, et augmente ainsi le potentiel de gravité de la maladie. Au site sableux, c'est la survie des sclérotes qui influencerait le développement de la maladie, alors que l'interaction de la rotation 3 ans de maïs et de l'amendement organique contribuerait à réduire la survie des sclérotes malgré l'absence d'effet significatif de l'ANOVA. La complémentarité des approches uni- et multivariables mises en œuvre pour tester l'effet des traitements de rotation et de fertilisation a résulté en une meilleure exploitation des données disponibles et a justifié l'approfondissement de l'analyse multivariable des données dans les chapitres 2 et 3.

L'étude de l'impact de pratiques culturales sur les caractéristiques physico-chimiques et microbiologiques du sol, du point de vue de la santé du sol (Chapitre 2), a montré un effet significatif et positif de l'amendement en compost urbain sur les caractéristiques physiques (stabilité structurale et capacité de rétention en eau accrues) et chimiques (plus forte teneur en C et N total) des deux sols amendés par rapport à la fertilisation minérale. L'effet des rotations et de l'amendement en compost urbain sur l'abondance bactérienne du sol était moins marqué que l'effet sur les caractéristiques physico-chimiques, et plus variable d'une année à l'autre.

Les régressions multiples et les ACR ont contribué à préciser les effets des traitements de rotation et de fertilisation sur la gravité de la sclérotinose par la construction de modèles minimaux qui regroupent les variables clés du développement de la maladie. Au site argileux, la rotation a entraîné une réduction de la gravité de la maladie principalement associée au rendement accru du soja et à la diminution de la biomasse des dicotylédones, dont la contribution au couvert végétal favorise le développement des apothécies. L'effet positif (« *conducive* ») du compost urbain sur la gravité de la sclérotiniose du soja au site argileux pourrait s'expliquer par l'amélioration du drainage en surface associée à l'amélioration de la structure du sol provoquée par l'apport de MO. En effet, la proportion élevée d'argile dans ce sol maintient un potentiel matriciel élevé et des conditions d'anoxie défavorables à la survie des sclérotes (Teo et Morrall, 1985b). De plus, la teneur accrue en N minéral est associée à une réduction de la survie des sclérotes en parcelles sous fertilisation minérale comparées aux parcelles sous amendement en compost urbain (Tenuta et Lazarovits, 2002). Au site sableux, la teneur accrue en argile favorisait au contraire la production d'apothécies et la gravité de la sclérotiniose, puisque l'humidité était «limitante» dans ce sol à la différence du loam argileux (Teo et Morrall, 1985b). Au site sableux, la production d'apothécies était en revanche contrée par une meilleure stabilité structurale et l'activité microbiologique qui y était associée, ces deux variables étant associées au compost urbain et à la rotation de 3 ans avec le maïs.

Les modèles minimaux ont ainsi permis de mieux comprendre les effets de la rotation et de l'amendement en compost urbain et de leur interaction avec les caractéristiques physico-chimiques et microbiologiques propres à chacun des sites. La forme partielle de la régression ou de l'ACR a identifié les variables qui étaient corrélées directement à l'effet de la rotation et de la fertilisation, mais aussi celles qui partageaient une structure spatiale commune avec les variables de la sclérotiniose. L'intégration de l'autocorrélation spatiale étant essentielle à une interprétation rigoureuse des données écologiques (Legendre et Legendre, 1998; Legendre et Trousselier, 1988),

l'effet de la structure spatiale sur les variables de la sclérotiniose a été approfondi dans le dernier chapitre de la thèse (Chapitre 3).

L'approche par la partition de variance (Chapitre 3) visait à améliorer la compréhension de l'effet de chacun des facteurs estimés de l'environnement (couvert végétal, physico-chimie et microbiologie du sol), de leur interaction et de leur relation avec la structure spatiale des variables de la sclérotiniose. Cette approche visait à confirmer ou infirmer l'effet des variables séparées incluses dans les modèles additifs, développés au chapitre 2, et de mieux comprendre leurs interactions. Dans le loam argileux, la partition de variance a montré que la réduction de la gravité de la maladie par la rotation avec le maïs était principalement attribuable aux effets de la rotation sur les caractéristiques du loam argileux et du couvert végétal. Ceci était appuyé par le fait que la structure spatiale de la production d'apothécies était largement expliquée par la structure spatiale des caractéristiques physico-chimiques du sol (Boland et Hall, 1988b) et du couvert végétal (Teo et *al*., 1989). En revanche, l'absence de structure spatiale de la gravité de la sclérotiniose en opposition à la structure spatiale dominante des apothécies a contribué à expliquer la faible corrélation entre les variables de sclérotiniose dans le loam argileux. Ces analyses de partition de variance permettent de conclure que les effets de la rotation sont surtout indirects, créant des conditions dans le sol et le couvert végétal défavorables au développement des apothécies du *S. sclerotiorum.* Ainsi, la rotation créerait indirectement des conditions défavorables au développement de la sclérotiniose chez le soja. De surcroît, la partition de variance montrait que la structure spatiale des apothécies était largement expliquée par celle de la survie des sclérotes, elle-même principalement expliquée par les caractéristiques physico-chimiques du sol. Boland et Hall (1988b) ont montré l'existence d'une structure spatiale commune aux apothécies et au développement de la maladie et suggéraient que des variables de sol en étaient à l'origine. Pour la première fois cette structure spatiale a été quantifiée et les variables de sols identifiées. La partition de la variance de l'association Apothécies-Survie révélait par ailleurs que l'activité microbiologique du sol, négativement reliée à la production d'apothécies dans les modèles additifs, ne semblait pas reliée directement aux variables de la sclérotiniose, mais qu'elle agissait plutôt en interaction avec les caractéristiques physico-chimiques du sol (Tokeshi et *al*., 1997). Au site argileux, l'association entre l'activité microbiologique et les variables de la sclérotiniose ne résulterait donc pas d'un lien de cause à effet mais plutôt d'une affinité commune avec certaines caractéristiques physico-chimiques des sols comme une texture plus grossière, la présence de MO ou une meilleure stabilité structurale, précédemment attribuée à l'application de compost urbain dans le chapitre 2. Au site sableux, contrairement au site loam

argileux, la structure spatiale de la gravité de la maladie était significative et principalement confondue avec la structure spatiale des caractéristiques physico-chimiques du sol et du couvert végétal. Le couvert végétal représenté par l'*A. artemisiifolia* n'était directement relié ni à la gravité de la maladie, ni à l'effet de l'interaction de la rotation avec l'amendement en compost, mais surtout confondu avec la structure spatiale des variables de sol. L'effet de l'interaction de la rotation avec l'amendement en compost était donc relié directement à la MO et indirectement au couvert végétal. Ces conclusions ont été renforcées par la partition de la variance de la germination carpogénique et de l'association DSI-Apothécies principalement expliquée par les caractéristiques physico-chimiques et microbiologiques du sol. L'effet suppressif sur la maladie était plus précisément attribué à une stabilité structurale accrue associée à une plus forte activité biologique (Tokeshi et *al*., 1997) et une plus forte concentration de la solution du sol en ions échangeables qui, ensemble, réduiraient la production d'apothécies (Singh et *al*., 1995). De plus, la partition de la variance de l'association Apothécies-Survie montrait un effet direct de l'activité microbiologique inhibitrice de la production d'apothécies mais cette activité était positivement corrélée à la survie des sclérotes. Ceci suggère une inhibition spécifique de la germination carpogénique par l'activité microbiologique du sol qui, indirectement, favoriserait la longévité des sclérotes en prolongeant leur dormance. Dans cette analyse, la survie des sclérotes était difficilement expliquée par les variables de chimie retenues, ce qui met en lumière les limites des méthodes statistiques utilisées au regard de la complexité de l'écologie du sol.

En conclusions, malgré certaines limites inhérentes aux méthodes d'analyse de données, les différentes approches utilisées dans cette étude ont permis d'approfondir les connaissances sur le développement de la sclérotiniose du soja et l'écologie du *S. sclerotiorum*. Ces approches ont été novatrices notamment grâce: au calcul de la contribution de chacun des traitements à la variance des variables de la sclérotiniose; à la sélection par les modèles additifs de variables clés qui expliquent le développement de la maladie et à l'approfondissement de leurs relations avec les pratiques culturales et la structure spatiale des données; enfin, à la partition de variance qui a permis de quantifier la part de variance de chaque composante étudiée et de proposer de nouvelles hypothèses sur leurs interactions et leur implication dans le développement de la sclérotiniose du soja.

Pour la première fois, on a démontré, chez deux sols, les effets suppressifs de la fertilisation organique ou de la rotation avec une espèce non-hôte ou encore de leur interaction sur la sclérotiniose du soja. Les effets suppressifs sur l'agent pathogène et la maladie se sont exprimés par

les interactions entre les différents facteurs de l'agroécosystème (Asirifi et *al*., 1994; Nakasone et *al*., 1999). En revanche, l'effet était parfois favorable (« *conducive* ») (Ferraz et *al*., 1999) à la maladie, montrant ainsi la nécessité de bien connaître les conditions locales avant d'élaborer des moyens de lutte pour juguler une infestation.

Cette étude approfondie des interactions entre les pratiques culturales, le sol et le couvert végétal permet de mieux cerner la complexité des phénomènes impliqués et en particulier l'ubiquité des interactions entre l'activité microbiologique du sol (abondance bactérienne et QMC notamment), les caractéristiques physico-chimiques du sol et le couvert végétal. Les résultats novateurs de cette thèse abondent dans le sens de la théorie écologique selon laquelle la biodiversité et la complexité des interactions sont nécessaires à l'équilibre des écosystèmes (Odum, 1969). Cette recherche corrobore le potentiel d'utilisation des agents pathogènes comme indicateurs de déséquilibres (ou d'équilibres) au sein des écosystèmes, tant agricoles que naturels (Hornby et Bateman, 1997; Howard, 1971; Rusch, 1972).

Les résultats de ces recherches ouvrent les perspectives suivantes:

- Au plan de la recherche fondamentale, promouvoir l'application des méthodes d'analyse multidimensionnelle à d'autres maladies et agents pathogènes telluriques des grandes cultures
- Au plan de la recherche appliquée et de la vulgarisation scientifique, mettre en œuvre des recherches aux fins du développement d'un Guide d'utilisation de la rotation et de l'amendement en compost urbain chez le soja au Québec
- Au plan personnel, joindre une équipe de recherche internationale qui œuvre en conservation (santé) des sols et en santé des cultures et y approfondir une expertise sur les indicateurs de la santé des agrosystèmes.

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ANNEXE A

A respiratory method to monitor soil or compost suppressiveness to *Sclerotinia sclerotiorum* under laboratory conditions. ***Rousseau, G.**, and Schaefer, R. Département de Phytologie, Pavillon Paul-Comtois, Faculté des sciences de l'agriculture et de l'alimentation, Université Laval, Quebec City, QC, Canada G1K 7P4, and (R.S.) Laboratoire d'Écologie des Sols Tropicaux, IRD Bondy, 32 avenue Henry Varagnat, 93143 Bondy Cédex, France.*

Sclerotinia stem rot or white mold, caused by *Sclerotinia sclerotiorum*, is one of the most significant diseases of soybean (*Glycine max*) in Northeastern America. Intensified soybean production, associated with less rotations and the use of mineral fertilizers instead of organic fertilization, can explain this increasing occurrence of white mold. It is hypothesized that compost can suppress white mold. Our objective was to develop a simple method to monitor soil (compost amended or sterilized soils) suppressiveness against *S. sclerotiorum* in soybean, in relation to microbial counts, soil type and physical and chemical soil characteristics under laboratory conditions. Soil respiratory quotient dynamic was assessed with a modified respiratory method extracting CO_2 by vaccuum. After incubation for 41 days, soil sterilization had no significant effect on sclerotia survival, nor did soil type ($P > 0.05$). Compost alone and soil compost amendment both significantly reduced sclerotia survival ($P < 0.001$ and $P = 0.013$, respectively). Sclerotia survival was not correlated with soil respiration. However, survival was negatively correlated with microbial counts ($r_p = -0.48$; $P < 0.001$) ; survival was also negatively correlated with organic matter content ($r_p = -0.46$; $P = 0.001$) for which gradient represented the first axis of redundancy analysis, pH ($r_p = -0.61$; $P < 0.001$) representing the second axis. This respiratory method along with redundancy analysis yielded new information about compost amended soil suppressiveness against *S. sclerotiorum.*

Keywords: *Sclerotinia sclerotiorum*, compost, suppressiveness, respiratory quotient, redundancy analysis.

Assessment of soil or compost suppressiveness to *Sclerotinia sclerotiorum* under growth chamber condition: correlations with laboratory and field assessments. ***Rousseau, G.***, *Rioux, S., and Dostaler, D. Département de Phytologie, Pavillon Paul-Comtois, Faculté des sciences de l'agriculture et de l'alimentation, Université Laval, Quebec City, QC, Canada G1K 7P4, and (S.R.) CEROM, Complexe scientifique, 2700, rue Einstein, Sainte-Foy, QC, Canada G1P 3W8*

Sclerotinia stem rot or white mold, caused by *Sclerotinia sclerotiorum*, is one of the most significant soybean (*Glycine max*) diseases. *S. sclerotiorum* sclerotia can survive 8 years in soil. Compost often reduces sclerotia survival, but can also enhance soil-borne disease development. Our objectives were to characterize soil and compost suppressiveness by soil type, physico-chemical characteristics and respiratory quotient in growth chamber. This 18 months growth chamber incubation was compared with a 41 days laboratory incubation and a 4 years field experiment. Compost enrichment significantly reduced survival ($P < 0.001$) after 18 months and survival was significantly lower in sandy loam than in clay loam ($P < 0.01$). Sclerotia survival after 4 months in growth chamber was correlated with laboratory survival ($r_p = 0.66$; $P = 0.02$) but not with field survival. In growth chamber, redundancy analysis showed an organic matter gradient on first axis (48.3% of survival and fructification variance). Organic matter was negatively correlated with survival and respiratory quotient, as in laboratory and field. Second axis (28.0%) was characterized by a sand-clay gradient, clay being correlated with survival and sand with fructification. Redundancy analysis showed significant correlation between soil and pathogen variables ($P < 0.05$) in all experiments. Field and controlled experiments, along with redundancy analysis, yielded new information underlying white mold suppression provided by compost.

Keywords: *Sclerotinia sclerotiorum*, compost, suppressiveness, redundancy analysis

ANNEXE B

Average values of selected physico-chemical and microbiological properties of the Conporec urban compost, analysed by CRIQ laboratory (Sainte-Foy, QC), in 1999.

	Urban Compost [z]			
Soil variables	**Mean**	**Min**	**Max**	**Med**
Physical				
OM (%)[w]	72.1	68.8	74.0	72.7
FC (%)[v]	131.6	132.7	158.2	132.7
Chemical				
pH	7.5	6.8	7.8	7.6
CEC (meqL-1)[u]	99.5	89.5	112.	98.1
total C (%)[t]	35.1	30.6	37.1	36.3
total N (%)	1.21	1.16	1.23	1.23
C/N	29.0	24.9	31.9	29.6
total S (%)	-	-	-	-
P (ppm) [s]	2218	2009	2509	2178
K (ppm)	6498	5929	7011	6526
Ca (ppm)	28912	25321	33379	28474
Mg (ppm)	2610	2369	2919	2575
Al (ppm)	-	-	-	-
Microbial activity				
CMQ [r]	0.02	0.01	0.02	0.02
PS1 (10^6 cellsmL^{-1})[q]	100.4	57.3	306.7	92.0
PS2 (10^6 cellsmL^{-1})[q]	117.0	49.3	205.3	112.0
BFI	0.22	0.01	0.48	0.06

[z] Urban compost (Conporec inc.) samples (n=4) were analysed once in 1999 by CRIQ laboratory (Sainte Foy, Canada) according to BNQ standards for compost quality (CAN/BNQ 1996)

[w] OM : Organic Matter (%) = (weight at 105°C-weight at 420°C)/(weight of air dried soil) * 100 (CPVQ, 1988)

[v] FC : Field Capacity (Cassel and Nielsen, 1986)

[u] CEC : Cation Exchange Capacity was calculated : CEC(meq/100) = [(7.5 - pH buffer) * 9] + [K] + [Ca] + [Mg] (AFEQ, 1990)

[t] C, N, S concentrations determined by LECO CNS 2000 ®

[s] P, K, Ca, Mg, Al determined by Mehlich III extraction method

[r] CMQ : C Mineralization Quotient, in 10-20 cm soil depth, after 41d soil incubation at 28°C, CMQ = (mg C/ mg C total) * 100

[q] Bacterial cells direct counts with Neubauer haemocytometer of soil (10-20 cm) suspension filtrate after 48h incubation at 28°C, in a physiologic saline solution (PS1) or, in a physiologic saline solution plus 5 gL^{-1} Lactose and 5 gL^{-1} Dextrose (PS2) (Rusch, 1972)

[p] BFI : Biological Fertility Index (Rusch, 1972).

ANNEXE C: Effet de l'amendement en compost urbain de deux sols sur la survie et la germination carpogénique des sclérotes du *Sclerotinia sclerotiorum,* en chambre de croissance et au laboratoire

Introduction

L'effet des composts et amendements organiques sur les agents pathogènes telluriques des plantes est fort documenté (Lazarovits, 2001). Or, la contribution d'amendements organiques à la répression de maladies des plantes est vue avec un certain scepticisme (Bailey et Lazarovits, 2003), notamment parce que les résultats expérimentaux sont difficilement reproductibles (Lazarovits, 2001). L'essentiel des études qui proposent des explications aux effets dits « suppressifs » de maladies par des amendements organiques (Boulter et *al*., 2000; Mitchell et Wheeler, 1990; Nico et *al*., 2003 ; Reuveni et *al.* 2002) a été réalisé en conditions contrôlées alors que tardent les résultats et preuves tangibles au champ (Grogan, 1979 ; Lazarovits, 2001). La plupart des recherches sur les amendements organiques réalisées chez le *S. sclerotiorum* (Asirifi et *al*., 1994 ; Kokalis-Burelle et Rodriguez-Kabana, 1994 ; Nakasone et *al.*, 1999 ; Tokeshi et *al*., 1997 et Viana et *al*., 2000) et autres *Sclerotinia* spp. (Lumsden et *al*., 1986 ; Wong et Willetts, 1975) reposent sur l'hypothèse que l'effet des amendements organiques sur les agents pathogènes est associé à l'activité biologique des substrats. Si on souhaite que soient corroborés au champ les résultats obtenus en conditions contrôlées et si l'on entend contribuer à l'explication des phénomènes associés aux probables effets « suppressifs » d'un amendement organique, il apparaît nécessaire d'améliorer les méthodes de recherche et d'analyse de données dans ces environnements.

On peut présumer que le compost urbain réprime la survie des sclérotes et la germination carpogénique du *S. sclerotiorum*, agent de la sclérotiniose du soja. Cette hypothèse est associée aux objectifs suivants : 1) préciser l'effet d'un compost urbain (Conporec Inc.), de deux sols (loam sableux, loam argileux) et du mélange de ces sols et du compost urbain sur la survie et la germination carpogénique (formation d'apothécies) de sclérotes du *S. sclerotiorum* en cabinet de croissance et au laboratoire ; 2) évaluer la survie des sclérotes tout en mesurant la respiration dans les deux sols (loam sableux, loam argileux) au laboratoire.

Les mesures de la respiration des sols et du compost urbain au laboratoire visent à éprouver la méthode de respirométrie proposée par R. Schaefer (communications personnelles) et décrite par Mboukou-Kimbatsa (1997). Le dégagement de CO_2, évalué par la méthode de respirométrie de Schaefer, est un indice reconnu pour estimer la décomposition de la matière MO (Anderson, 1982) et pour déterminer l'activité biologique globale du sol (Bachelier, 1968). Cette annexe présente des expériences en conditions contrôlées en complément des chapitres de la thèse qui couvrent la recherche au champ sur l'effet de la rotation maïs-soja et de l'amendement en compost urbain sur la sclérotiniose du soja dans deux sols du Québec.

Matériel et Méthodes

Échantillons de sols et de compost urbain

Deux expériences au laboratoire et en cabinet de croissance ont porté sur un compost urbain, deux sols et des mélanges sols-compost urbain. Le compost urbain a été produit et fourni par l'entreprise Conporec inc. de Tracy QC (Conporec, 2004). Les échantillons de sols ont été prélevés entre le 1er et le 9 juillet 1999 dans les unités expérimentales de l'expérience de champ traitée dans les chapitres 1 à 3, expérience mise en oeuvre de 1999-2002 à la station de recherche IRDA-CÉROM (Institut de Recherche et de Développement en Agroenvironnement ; Centre de recherche sur les grains inc.) de Saint-Hyacinthe QC, sur un loam argileux de la série Saint-Urbain et sur un loam sableux de la série Saint-Damase.

Les échantillons de loam argileux et de loam sableux ont été prélevés à l'aide d'une tarière dans les horizons 0-10 cm et 10-20 cm. Chaque échantillon était constitué de trois sous-échantillons prélevés dans trois quadrats de 0,5 m^2 disposés le long d'une diagonale nord-sud dans chaque parcelle en fertilisation minérale. Les échantillons étaient séchés à l'air et tamisés à 2,8 mm avant leur transfert au laboratoire. Des échantillons moyens des parcelles en fertilisation minérale de chaque sol ont été utilisés pour préparer les substrats pour les expériences en conditions contrôlées.

Dispositifs expérimentaux

Les deux expériences en conditions contrôlées ont été disposées selon un plan en tiroirs subdivisés (split-plot) avec trois blocs. Les unités expérimentales étaient des pots de 165 mm de diamètre en cabinet de croissance. Le facteur substrat était en parcelles principales avec cinq substrats : le compost urbain seul, le loam argileux, le loam argileux additionné de 50 % (v/v) de compost urbain, le loam sableux seul et enfin le loam sableux additionné de 50 % (v/v) de compost urbain. Le facteur stérilisation était en sous-parcelles : substrats stérilisés ou substrats non stérilisés. La stérilisation a été faite à l'autoclave (15 min, 121˚C) pour les substrats de l'expérience au laboratoire, et par l'injection de vapeur pendant 1 h pour les substrats destinés à l'expérience en chambre de croissance.

Caractérisation du compost urbain et des échantillons de sols

Les sols, le compost urbain et les mélanges sol-compost urbain ont préalablement été caractérisés par leurs principales caractéristiques physico-chimiques avant incubation au laboratoire ou en cabinet de croissance. La capacité au champ a été réalisée au laboratoire. La détermination de la teneur en MO, du pH et de la teneur en P, K, Ca, Mg et Al a été confiée au laboratoire Agridirect de Longueuil QC. Les mesures de granulométrie, les teneurs de C et d'N ont été réalisées au département des sols et de génie agroalimentaire de l'Université Laval. Les unités de mesure, les abréviations et les références des méthodes d'analyses physico-chimiques et microbiologiques sont regroupées dans le Tableau 1.

Essai au laboratoire: analyses microbiologiques (respirométrie et comptages bactériens) des substrats et survie des sclérotes

Au laboratoire, les substrats ont été soumis aux analyses microbiologiques: la respirométrie (méthode de R. Schaefer, décrite par Mboukou-Kimbatsa (1997) et adaptée par Rousseau et Schaefer, 2003, Annexe A), et les comptages bactériens (méthode de Rusch, 1972). On a également déterminé la survie des sclérotes à la fin de l'expérience. Cette expérience visait dans un premier temps à caractériser l'activité microbiologique des substrats utilisés en cabinet de croissance puis, dans un second temps, à estimer la survie des sclérotes dans ces substrats à court terme et en suivant l'évolution de l'activité respiratoire.

Respirométrie

La méthode de respirométrie de Mboukou-Kimbatsa (1997) adaptée par Rousseau et Schaefer (2003) a été utilisée pour mesurer le dégagement de CO_2 des substrats de sols seuls, de compost urbain seul, de sol additionné de compost urbain et d'un traitement témoin de sable standard (Ottawa), incubés en erlenmeyers au laboratoire. Soixante g des substrats (25 g pour le compost urbain seul) humidifiés à 80 % de la capacité au champ (Cassel et Nielsen, 1986) ont été forcés au travers d'un tamis de 2 mm; les substrats tamisés ont été déposés dans des flacons erlenmeyers de 250 mL qui constituaient alors les unités expérimentales. Par rapport à la méthode décrite par Mboukou-Kimbatsa (1997), le volume de substrat-sol a été réduit de 150 à 60 g. Des sclérotes du *S. sclerotiorum* non stérilisés en surface ont été imbibés durant 12 h dans de l'eau distillée stérile. Vingt (20) sclérotes ont été incorporés et mélangés aux 60 g des substrats en flacons erlenmeyers scellés hermétiquement, puis incubés en étuve (Blue M Dry Type Bacterial Incubator) à 28°C, à l'obscurité pour la durée de l'expérience. Les sclérotes du *S. sclerotiorum* provenaient du crible de grains de soja récoltés en 1999 dans la région de Saint-Césaire QC.

Le dégagement de CO_2 a été estimé après 5, 14, 26 et 41 j d'incubation. Pour ce faire, les flacons erlenmeyers hermétiques utilisés pour l'incubation étaient reliés à un système de trompe à vide. Le CO_2 des substrats est extrait grâce au vacuum (-2000 à -2500 kPa) créé par la dépression de la trompe à vide qui fait passer l'air extrait des substrats successivement dans deux erlenmeyers à bec de 125 mL remplis d'une solution alcaline de barite hydratée [hydroxide de barium / $Ba(OH)_2$] qui fixe le CO_2 et précipite sous forme de $BaCO_3$. L'extraction par vacuum a été appliquée à deux reprises à chaque substrat en erlenmeyer. Entre les extractions, l'atmosphère était remplacée par de l'air sans CO_2 grâce à l'emploi d'un filtre d'Ascarite II. Par rapport à la méthode décrite par Mboukou-Kimbatsa (1997), les tubes de verre de solution de $Ba(OH)_2$ ont été remplacés par des erlenmeyers de 125 mL. Ainsi, après avoir fait deux fois le vide dans le système, le $Ba(OH)_2$ est stocké dans des récipients de verre fumé hermétiques (le $BaCO_3$ est instable à la lumière) puis titré avec de l'acide oxalique dihydraté N/22 (2,0919 g L^{-1}). Les tubes d'aération immergés dans le $Ba(OH)_2$ étaient fermés par un embout de pipette pour assurer un diamètre régulier des bulles d'air. En résumé, le CO_2 des substrats en erlenmeyers est extrait par vacuum et capté par la solution de $Ba(OH)_2$, puis titré à l'acide oxalique. Le quotient de minéralisation du carbone (QMC) a enfin été

calculé: QMC = (C du CO_2 / C total du sol)*100 (Dommergues, 1960), le C total du sol étant déterminé par LECO CNS 2000 ®.

Comptages bactériens

Deux séries de comptes bactériens, par une méthode adaptée de Rusch (1972), ont été effectuées sur des suspensions de substrat remis en incubation dès la fin de leur incubation au laboratoire (41^e jour). Dix g des substrats frais sol ou sol + compost urbain (ou encore 20 g pour le compost urbain seul) ont été mis en suspension et agités pendant 10 min à 250 rpm, en erlenmeyers de 250 mL, dans 50 mL (100 mL pour le compost urbain) d'une solution saline physiologique (7 gL^{-1} NaCl). La solution saline physiologique était non additionnée (série de comptages bactériens 1) ou additionnée de 5gL^{-1} de lactose et 5gL^{-1} de dextrose (série de comptages bactériens 2). Après 48 h d'incubation sans agitation dans les solutions salines à 28˚C, en étuve à l'obscurité, les suspensions de substrats ont été filtrées sur papier filtre Whatman # 1. Le volume de filtration était limité à 2-3 mL pour prévenir la dégradation des filtres. Les filtrats de suspension de cellules bactériennes ont été dilués au besoin et les cellules bactériennes ont été comptées directement sur hémacytomètre de Neubauer en microscopie photonique. Les comptes bactériens ont été exprimés en nombre de cellules mL^{-1} de suspension.

Survie des sclérotes

Par tamisage des sclérotes des unités expérimentales, la survie (%) des sclérotes a été estimée 42 j après le début de l'expérience au laboratoire. Les sclérotes qui avaient conservé leur fermeté sont considérés viables (van Toor et *al*., 2000).

Essai en cabinet de croissance: survie et germination carpogénique des sclérotes

En cabinet de croissance (Conviron ; Controlled Environments Limited, Winnipeg), 20 sclérotes non stérilisés en surface et préalablement imbibés durant 12 h dans de l'eau distillée stérile, ont été placés dans des pots (30 pots) de 16 cm x 20 cm, remplis du substrat sol, compost urbain ou mélange sol-compost urbain, stérilisés ou non. Les pots individuels constituaient les unités expérimentales. Huit (8) cm d'épaisseur de perlite ont d'abord été placés dans les pots pour assurer un bon drainage, puis les substrats ont été ajoutés sur une épaisseur de 10 cm. Les sclérotes étaient incorporés dans les cinq premiers cm du substrat. Les pots étaient arrosés jusqu'à saturation une fois par semaine. Les conditions d'incubation étaient maintenues optimales pour la germination

carpogénique du *S. sclerotiorum* (Hall, 1994) avec 12 h de photopériode (350 $\mu Em^{-2}sec^{-1}$ pour la densité du flux de photon photosynthétique disponible, % DFPP), 22°C le jour et 16°C la nuit. Les sclérotes du *S. sclerotiorum* provenaient du crible de grains de soja récoltés en 1999 dans la région de Saint-Césaire QC. Les adventices étaient arrachées à chaque semaine.

La survie des sclérotes a été évaluée par tamisage des cinq premiers cm de substrat après 4 et 18 mois d'incubation en cabinet de croissance (Conviron); les sclérotes récupérés qui avaient conservé leur fermeté étaient considérés viables (van Toor et *al*., 2000) et replacés dans les pots avec leur substrat d'origine pour la seconde évaluation. La germination carpogénique a été déterminée par le nombre d'apothécies produites par unité expérimentale : les apothécies étaient comptées à chaque semaine avant l'arrosage des pots et, à la fin de l'expérience, on a fait la somme des apothécies dénombrées au cours des 18 mois.

Analyses statistiques

La normalité des données a été testée par la procédure PROC CAPABILITY du progiciel Statistical Analysis System (SAS pour Windows V8, SAS Institute Inc. 2001). L'homogénéité de la variance a été vérifiée par les procédures PROC GLM et PROC PLOT du progiciel SAS. Les variables dont la distribution n'était pas normale ont été transformées (Underwood, 1997).

Analyses univariables

L'effet du type de sol, de l'amendement et de la stérilisation sur les caractéristiques physico-chimiques et microbiologiques des substrats, la survie et la germination carpogénique des sclérotes ont été testés par l'analyse de variance (ANOVA) et des tests de contrastes qualitatifs de la procédure PROC GLM (SAS pour Windows V8, SAS Institute Inc. 2001). Les effets étaient considérés significatifs au seuil $P < 0,05$. Des corrélations de Pearson entre la survie des sclérotes au laboratoire et la survie et la production d'apothécies en cabinet de croissance ont été calculées par la procédure PROC CORR du progiciel SAS. Les corrélations étaient significatives au seuil $P < 0,05$.

Analyses multivariables

L'analyse canonique des redondances (ACR) (van den Wollenberg, 1977) a été utilisée pour expliquer les variables de survie des sclérotes, de QMC et de comptes bactériens (variables explicatives; matrice Y) de l'essai au laboratoire. En cabinet de croissance, les variables à expliquer étaient la survie des sclérotes après 4 et 18 mois d'incubation, la germination carpogénique après 18

mois d'incubation, le QMC et les comptes bactériens. Dans les deux expériences, les variables physico-chimiques (Heq, argiles, limons, sables, pH, C, N, C/N, P, K, Ca, Mg, Al, MO, CEC) formaient la matrice des variables descriptives (matrice X) (Legendre et Legendre, 1998). On n'a conservé dans le modèle que les variables descriptives dont la contribution marginale (la fraction de chaque variable utilisée seule dans l'analyse) était élevée, c'est à dire les variables qui prises seules expliquent une forte proportion de la variance de Y. Cette proportion dépendait de la matrice Y à expliquer. On a ainsi construit empiriquement un modèle significatif au seuil $P < 0,05$. Cette sélection de variables descriptives a été faite avec la procédure *Forward Selection* du logiciel CANOCO 4.5 (ter Braack et Smilauer, 2002).

Résultats

Caractéristiques physico-chimiques des substrats

Les analyses des substrats avant incubation (résumé des méthodes d'analyse au Tableau 1) montrent des différences significatives entre les substrats pour toutes les variables physico-chimiques (Tableau 2). Les substrats diffèrent significativement par la granulométrie (argile, limon, sable), la teneur en MO et l'humidité équivalente (Heq). Le compost urbain seul a la plus haute teneur en MO. Or, la teneur en MO ne diffère pas entre les sols seuls (loam argileux et loam sableux). L'amendement des sols en compost urbain augmente significativement leur teneur respective en MO. Le substrat *loam argileux-compost urbain* a une teneur en MO significativement plus élevée que le substrat *loam sableux-compost urbain*. La capacité de rétention en eau des substrats, estimée par l'humidité équivalente (Heq), diffère significativement chez tous les substrats. L'Heq est maximale chez le compost urbain seul et minimale chez le loam sableux seul ; sont intermédiaires en Heq, et par ordre croissant, le substrat *loam sableux-compost urbain*, le loam argileux seul et le substrat *loam argileux-compost urbain* (Tableau 2).

Le pH est maximal chez le compost urbain seul et chez le substrat *loam sableux-compost urbain* (Tableau 2). La CEC est maximale dans le compost urbain et significativement moindre dans le loam sableux. La CEC est semblable chez les deux substrats *sol-compost urbain* (Tableau 2). Les teneurs en C et N diffèrent significativement entre les substrats, et les substrats se classent dans le

même ordre pour la teneur en ces deux éléments : le compost urbain est le plus riche, suivi du substrat *loam argileux-compost urbain*, du *loam sableux-compost urbain*, du loam sableux et enfin du loam argileux (Tableau 2). Le rapport C/N est supérieur dans le compost urbain seul et dans le loam sableux par rapport au substrat *loam sableux-compost urbain*, au loam argileux et au substrat *loam argileux-compost urbain.* La teneur en K et Ca est plus élevée dans le compost urbain que dans les autres substrats. La teneur en Al est maximale dans le loam sableux, tous les substrats étant significativement différents entre eux (Tableau 2).

Essai au laboratoire

Microbiologie : respirométrie et comptages bactériens

Respirométrie. Le quotient QMC a été estimé par le dégagement de CO_2 (respirométrie) après 5, 14, 26 et 41 j d'incubation en erlenmeyers au laboratoire. Au 41^{e} jour, le QMC diffère significativement entre les substrats (Tableau 2). Le QMC est maximal dans le loam argileux seul, suivi du loam sableux seul, des substrats *sol-compost urbain* puis du compost urbain seul (Tableau 2). Sur l'ensemble des 41 j de l'expérience, la stérilisation du substrat réduit significativement le QMC chez tous les substrats, sauf chez le substrat *loam sableux-compost urbain* où la stérilisation n'a pas d'effet (Fig. 1).

Comptes bactériens. À la fin de l'expérience (au 41^{e} j), après incubation des substrats durant 48 h dans une solution physiologique additionnée de lactose 5 gL-1 et de dextrose 5 gL-1 (*Comptages bactériens 2*), les comptes bactériens (en nombre de cellules bactériennes·mL^{-1}) diffèrent significativement d'un substrat à l'autre. Les comptes bactériens sont maximums dans le compost urbain seul, puis diminuent dans l'ordre des substrats *loam sableux-compost urbain*, *loam argileux-compost urbain*, loam argileux seul puis loam sableux seul (Tableau 2). Les comptages bactériens 1 dans une solution physiologique non additionnée de lactose/dextrose ne sont pas significatifs. La stérilisation du substrat n'avait par ailleurs pas d'effet significatif sur les comptes bactériens 1 ou 2.

Survie des sclérotes

Les loam argileux et le loam sableux montrent la plus forte survie des sclérotes (Tableau 3). La survie des sclérotes est réduite (P = 0,05) dans le compost urbain et le *loam argileux-compost urbain* par rapport aux sols seuls (loam argileux ou loam sableux). L'ajout de compost au loam sableux ne

réduit pas (P = 0,07) la survie des sclérotes. De même, la stérilisation des substrats n'a pas d'effet significatif sur la survie des sclérotes.

Analyse canonique des redondances sur la survie des sclérotes et l'activité microbienne des substrats

Le premier axe canonique de l'ACR sur la survie des sclérotes, le QMC et les comptages bactériens au laboratoire explique 66,5 % de la variation de la matrice explicative (Y) (Fig. 2). Ce premier axe canonique montre une opposition entre les variables associées à la MO (Heq, pH, C, N, CEC, Ca) et les variables associées à la granulométrie (argile, limon, sable, Al). Ce contraste est particulièrement visible chez les points représentant les objets (unités expérimentales) qui sont répartis sur ce premier axe canonique selon leur teneur en MO. Le second axe canonique explique 14,4 % de la variance de la matrice Y, et montre également une opposition des variables associées à la granulométrie et de quelques variables associées à la MO (Heq, C, N). Ce deuxième axe montre de plus une discrimination des objets par la stérilisation. Cette distinction est particulièrement marquée chez les substrats *sol-compost urbain*, et dans une moindre mesure, chez le loam sableux, i.e. les objets représentant les substrats non-stériles se situent surtout dans la partie supérieure du plan (au-dessus du premier axe), qui correspond à la section positive du deuxième axe, tandis que les substrats non-stériles se situent plutôt dans la partie inférieure du plan (Fig. 2).

La survie des sclérotes en laboratoire est corrélée négativement aux deux premiers axes canoniques (Fig. 2). Sur le premier axe canonique, la survie des sclérotes est négativement corrélée à la teneur en MO représentée principalement par les teneurs en C et N, ainsi que par les autres variables associées au compost urbain (pH, Ca, CEC, Heq), variables corrélées positivement au premier axe canonique (Fig. 2). L'effet de la MO exprimé par ce premier axe canonique est associé au nombre de cellules bactériennes dans le substrat (*Comptages bactériens 2*) (Fig. 2). En revanche, le quotient de minéralisation du carbone (QMC) est négativement corrélé à la teneur en MO et plutôt associé aux sols non-amendés en compost urbain. En effet, les objets représentant les sols seuls sont également associés à cette section négative du premier axe (section du plan à gauche du second axe). Le QMC est associé à la survie des sclérotes. Sur le deuxième axe canonique, la survie des sclérotes est associée à la stérilisation des substrats, surtout chez les substrats *sol-compost urbain*, tel qu'illustré par la séparation entre les substrats stériles et non-stériles le long de ce deuxième axe. Les objets qui représentent les substrats stérilisés se situent surtout dans la section de plan définie par la section

positive du deuxième axe, i.e. à l'opposé du vecteur associé à la survie des sclérotes. Les variables de microbiologie quant à elles ne semblent pas affectées par la stérilisation du substrat tel que représentée par le deuxième axe canonique. En effet, les vecteurs représentant les comptages bactériens et le QMC ne sont que très peu corrélés au second axe canonique (Fig. 2).

Essai en cabinet de croissance

Survie et germination carpogénique des sclérotes

Après 4 mois d'incubation en cabinet de croissance, la survie des sclérotes est réduite significativement ($P < 0,05$) par les substrats avec compost urbain par rapport aux sols seuls (Tableau 4). Après 4 mois, la moyenne de survie des sclérotes est significativement ($P < 0,05$) plus élevée dans les substrats stérilisés que dans les substrats non-stériles. Après 18 mois d'incubation, aucun sclérote n'a survécu dans le loam sableux amendé en compost urbain (Tableau 4). La survie dans le loam argileux seul est significativement supérieure à celle des autres substrats (17,5 %), alors que la stérilisation n'a plus d'effet à 18 mois (Tableau 4).

La production d'apothécies après 18 mois d'incubation en cabinet de croissance était influencée significativement par les substrats en interaction avec la fertilisation. Le compost urbain, seul ou combiné, stérile ou non, est généralement associé à de faibles germinations carpogéniques (< 1 apothécies par traitement), alors que les loams seuls sont plutôt associés aux valeurs plus élevées (9,7 > nb d'apothécies par traitement > 3,7) (Tableau 4). Cependant, alors que l'amendement en compost réduit significativement le nombre d'apothécies dans le loam argileux sans effet significatif de la stérilisation, la stérilisation interagit avec le substrat dans le cas du loam sableux. Le loam sableux stérile n'est pas significativement différent du *loam sableux-compost urbain* non-stérile et le loam sableux non-stérile n'est pas significativement différent du *loam sableux-compost urbain* stérile (Tableau 4).

Analyse canonique des redondances sur la survie des slérotes, la production d'apothécies et l'activité microbiologique des substrats

Le premier axe canonique de l'ACR sur la survie des sclérotes, la production d'apothécies en cabinet de croissance, le QMC et les comptages bactériens explique 54,4 % de la variation de la matrice explicative (Y) (Fig. 3). Ce premier axe canonique montre une opposition entre les variables

associées à la MO (C, N, K, Heq, CEC) et les variables associées à la granulométrie (argile, sable). Les objets (unités expérimentales) se répartissent sur ce premier axe canonique en fonction de leur teneur en MO, i.e. les objets représentant les composts se situent dans la section de plan définie par la section positive du premier axe. Les mélanges sont regroupés autour de l'origine et les sols seuls se retrouvent dans la section de plan définie par la section négative du premier axe canonique (Fig. 3). Le second axe canonique explique 16,9 % de la variation de Y et montre un gradient de granulométrie, plus particulièrement une opposition argile-sable (Fig. 3). L'effet de la stérilisation est exprimé chez les substrats non amendés en compost urbain et en particulier chez le loam sableux seul, sol dont les objets sont distinctement séparés le long du second axe canonique selon qu'ils ont été stérilisés ou non (Fig. 3).

La survie des sclérotes après 4 mois d'incubation en cabinet de croissance est associée uniquement au premier axe canonique, alors que la survie des sclérotes après 18 mois est associée aux deux axes canoniques. La survie des sclérotes à 18 mois est également corrélée négativement à la teneur en MO (représentée par les variables qui lui sont associées: C, N, K, Heq, CEC), mais l'influence de la MO diminue par rapport à l'estimation précédente à 4 mois. L'argile et la survie des sclérotes sont liés et négativement corrélés aux deux axes canoniques à 18 mois, (voir « Argile » et « Survie 18 mois » dans la Fig. 3). Le somme des apothécies après 18 mois en cabinet de croissance est corrélée négativement au premier axe canonique et à la teneur en MO (Fig. 3). La germination carpogénique est corrélée positivement au second axe canonique, corrélée à la teneur en sable et associée aux objets représentant les substrats stériles (Fig. 3).

Les variables de microbiologie sont fortement corrélées au premier axe mais peu au second axe canonique (Fig. 3). En effet, les comptages bactériens (*Comptages* 2 ; Fig. 3) sont fortement associés à la MO et en particulier la teneur en C, N, K et à l'humidité équivalente (Heq). Le nombre de cellules bactériennes (*Comptages 2*) est négativement corrélé à la survie des sclérotes, à 4 mois surtout et à 18 mois, et à la production d'apothécies. En revanche, la minéralisation du C estimée par le quotient QMC est nettement associée à la survie (particulièrement à 4 mois) et à la production d'apothécies après 18 mois (*Apothécies* ; Fig. 3) en cabinet de croissance. Ainsi, le QMC est opposé à la teneur en MO et corrélée négativement au premier axe canonique (Fig. 3).

Discussion

Essai au laboratoire

La mesure de l'activité respiratoire comme estimation de l'activité biologique globale des substrats s'est révélée être un indicateur efficace et discriminant pour les types de sols comme l'ont estimé Dommergues (1960) et Bachelier (1968), mais aussi pour l'effet de l'amendement en MO (Tableau 2). En effet, seuls les substrats *sol-compost urbain* n'étaient pas différents pour le QMC. De plus, l'effet de la stérilisation sur le QMC était siginificatif dans tous les substrats sauf dans le substrat *loam sableux-compost urbain*, ce qui suggère que dans ce sol amendé l'activité microbiologique reprend plus vite après stérilisation que dans le loam argileux et même le compost seul.

Les comptages 2 réagissaient au type de substrat de manière opposée au QMC, i.e. là où le QMC est faible, les comptages montrent des nombres élevés de cellules (Tableau 2). Ceci est expliqué par la sensibilité de l'abondance bactérienne à la fraction labile de la MO qui permet une augmentation rapide du nombre de cellules, alors que la fraction plus récalcitrante de la MO n'a que peu d'impact sur le nombre de cellules à court terme.

Les effets du compost seul et en mélange avec le loam argileux sur la survie des sclérotes, permettent de conclure à la présence d'un effet suppressif du compost urbain pour ce sol. En revanche, dans le loam sableux on peut supposer que la poursuite de l'incubation au-delà de 41 j aurait amélioré la précision de l'estimation et permis de déceler un effet significatif de l'amendement.

La stérilisation au laboratoire n'avait pas d'effet significatif sur la survie des sclérotes, ce qui suggère dans un premier temps que la survie serait dépendante de la microflore associée aux sclérotes plutôt que de la microflore des substrats. Or, les conditions d'incubation (28˚C, 80 % de la capacité au champ), considérées comme optimales pour le développement de la microflore tellurique, pourraient expliquer l'absence d'effet de la stérilisation au laboratoire. En effet, ces conditions favorables au laboratoire auraient pu annuler les effets de la stérilisation en permettant une reprise rapide de

l'activité biologique puisque les substrats étaient en contact avec les sclérotes non-stériles et avec l'air ambiant lors du renouvellement de l'air des échantillons à chaque mesure de dégagement du CO_2. Dans cette expérience au laboratoire, la stérilisation des substrats n'aura pas permis de montrer une quelconque contribution de l'activité biologique à l'effet suppressif de la MO, contrairement à plusieurs expériences réalisées précédemment à ce sujet en conditions contrôlées (Kokalis-Burelle et Rodriguez-Kabana, 1994; Nakasone et *al.*,1999) ou en pots au champ (Mitchell et Wheeler, 1990). Cependant, dans une expérience en serre chez le *S. minor*, Nico et *al*. (2003) n'avaient pas pu établir de lien direct entre la mycoflore antagoniste et l'effet suppressif de deux amendements organiques frais ajoutés au sol (paille de luzerne et fumier de poulet).

Analyse canonique des redondances

Alors que l'analyse univariable ne montrait pas d'effet de la stérilisation et ne permettait pas de conclure à l'implication de l'activité biologique du substrat comme dans l'étude de Nico et *al*. (2003), l'ACR montre une corrélation négative significative entre la survie des sclérotes et le nombre de cellules bactériennes ($r_p = 0.58$; $P = 0.05$) (Fig. 2). La juxtaposition des variables de microbiologie et de la survie au laboratoire dans la matrice explicative a donc permis de confirmer l'implication de l'abondance bactérienne dans les phénomènes de suppression observés suite à l'amendement en MO. Cette implication suggère que la suppression est de type "général" ("*general suppression*"), telle que définie par Rovira et Wildermuth (1981), par opposition à la suppression dite "spécifique" ("*specific suppression*") attribuée à l'effet d'un ou plusieurs groupes de micro-organismes (Weller et *al*., 2002). En revanche, le QMC s'est révélé positivement corrélé à la survie ($r_p = 0{,}26$, $P = 0{,}08$) (Fig. 2) car sa valeur diminuait à mesure que la teneur en C total augmentait dans le substrat (Tableau 2), alors que la survie tendait à diminuer lorsque la teneur en MO était augmentée. En d'autres termes, l'apport de MO stable sous forme de compost urbain entraîne une forte diminution du QMC dans les substrats amendés alors que l'apport de MO labile associée, bien que faible en proportion, stimule le développement de l'abondance bactérienne. L'ACR illustre également le peu de poids de la granulométrie dans cette expérience par rapport à l'expérience en cabinet de croissance. En effet, les variables de granulométrie se montrent colinéaires (Fig. 2). Cette incubation à court terme (41 j) aura donc surtout permis de mettre en évidence et d'expliquer l'effet suppressif du compost urbain seul, ou en mélange, même si l'ANOVA suggère que cet effet est plus marqué dans le loam argileux que dans le loam sableux.

Essai en cabinet de croissance

L'effet de l'amendement en compost urbain montre un effet suppressif de la MO contre la survie et la germination des sclérotes chez les deux sols, alors que l'incubation au laboratoire ne montrait d'effet suppressif que du compost seul ou en mélange avec le loam argileux. Les deux substrats *sol-compost urbain* n'étaient cependant pas significativement différents du compost urbain seul, ce qui suggère qu'au-delà d'une certaine proportion de compost urbain, l'effet suppressif du substrat est maximale. Des expériences menées en serre par Nico et *al*. (2003) avec le *S. minor* montraient l'existence d'un seuil à partir duquel l'effet suppressif de la paille de luzerne et du fumier de poule devenait significatif par rapport au traitement témoin non amendé. Ainsi, l'incubation en cabinet de croissance, et dans une moindre mesure au laboratoire, permet de déterminer rapidement les proportions d'amendements organiques qui ont des effets significatifs, et peut ainsi être utilisée comme un crible avant d'entreprendre des essais à plus grande échelle.

Contrairement à l'incubation au laboratoire, l'effet de la stérilisation est significatif après 4 mois d'incubation en cabinet de croissance et permet de conclure à l'implication de la microflore dans les phénomènes de suppression de la survie des sclérotes sans le recours à l'ACR. Après 18 mois les substrats stérilisés atteignent un effet suppressif comparable à celui des substrats non stérilisés. La stérilisation ne ferait donc que retarder l'apparition de l'effet suppressif, intimement relié à la microflore, tel que suggéré par plusieurs auteurs pour le *S. sclerotiorum* (Nakasone et *al*., 1999; Tokeshi et *al*., 1997) ou le *S. homeocarpa* (Boulter et *al*., 2000). Après 18 mois, on constate également un taux de survie relativement élevé chez le loam argileux et nul chez le loam sableux amendé en compost urbain. Ceci suggère un effet "protecteur" de l'argile et un effet synergique entre le compost et le loam sableux, puisque les sclérotes sont tous éliminés dans le mélange, mais pas dans le compost seul ou le loam sableux seul. Puisque les pots n'étaient arrosés qu'une fois par semaine et séchaient en surface, la texture plus fine du loam argileux et sa capacité de rétention en eau plus élevée (Tableau 2) ont pu limiter les effets des cycles humidification-dessiccation, principaux responsables de la mort des sclérotes dans le sol, d'après Smith (1972). De plus, lorsqu'il est arrosé puis se dessèche, le loam argileux forme une croûte de surface, particulièrement épaisse et résistante dans le loam argileux non amendé, en raison de la destruction des agrégats par l'action de l'eau. Cette croûte forme une protection efficace des sclérotes contre l'action des cycles humidification-dessiccation et sa disparition suite à l'action de micro-organismes spécifiques

introduits dans le sol a été associée à un effet suppressif contre le *S. sclerotiorum* (Tokeshi et *al*., 1997). Chez le loam sableux amendé en compost urbain, la diminution de la survie des sclérotes serait due à la combinaison d'un apport massif de MO et d'une texture favorable au développement de la flore bactérienne. On constate en effet que le loam sableux amendé en compost urbain permet un meilleur développement de l'abondance bactérienne (Comptages 2) que les autres substrats, hormis le compost urbain seul (Tableau 2), cependant le QMC y est plus faible que dans les sols seuls, principalement en raison de la plus forte teneur en C total (Tableau 2). Ceci suggère, que la fraction la plus labile de la MO du compost urbain permet l'augmentation de l'abondance bactérienne, alors que l'augmentation de la fraction la plus stable induit une diminution du QMC. Ces deux fractions de la MO semblent interagir avec les propriétés physico-chimiques du sol et la microflore entraînant des effets suppressifs différents selon les substrats comme le suggèrent Tokeshi et *al*. (1997).

La germination carpogénique réagit différemment de la survie des sclérotes à la stérilisation (Tableau 4). Il se peut que la stérilisation ait modifié les propriétés physico-chimiques du loam sableux, comme par exemple une altération de sa structure due à la plus faible activité microbienne qui aurait permis la formation d'une croûte de surface défavorable à la germination des sclérotes ou à la levée des stipes formant les apothécies. Dans ce cas, l'activité des micro-organismes semble avoir eu l'effet inverse de celui décrit dans les substrats *sol-compost urbain*, et rapporté par Tokeshi et *al*. (1997), i.e. l'activité microbiologique aurait créé une structure plus favorable à la levée des stipes et donc à la formation d'apothécies.

Analyse canonique des redondances

En cabinet de croissance, on retrouve le même effet de la MO représenté par le premier axe canonique, et la même opposition entre les variables de microbiologie (*QMC* et *Comptages 2*) le long de cet axe que dans l'expérience au laboratoire. Dans cette expérience en cabinet, le QMC était significativement corrélé à la survie des sclérotes après 4 mois (r_p = 0,57, *P* = 0,01), 18 mois (r_p = 0,48, *P* = 0,007) et à la production d'apothécies (r_p = 0,45 *P* = 0,01) (Fig. 3). Ceci soutient l'effet favorable d'un QMC élevé sur le *S. sclerotiorum* suggéré par l'ACR sur les résultats au laboratoire (Fig. 2), ainsi que les différences significatives de QMC entre les substrats (Tableau 2). Cet effet est probablement attribuable à la faible proportion de MO stable par rapport à la MO labile indiquée par

le QMC élevé qui caractérise les sols seuls (Tableau 2) et en particulier le loam argileux dans lequel la survie des sclérotes est la plus élevée à l'issue de l'expérience (Tableau 4). Ces résultats appuient la nature générale de la suppression (Weller et *al*., 2002) tel que montrée précédemment par l'ACR sur l'incubation au laboratoire. De plus, l'effet significatif de la stérilisation en cabinet de croissance confirme l'implication de la biomasse bactérienne associée à la suppression dite générale (Rovira et Wildermuth, 1981). Sur le deuxième axe canonique l'effet de la granulométrie n'apparait qu'après 18 mois d'incubation et est surtout mis en évidence par la corrélation de la survie des sclérotes à 18 mois avec la teneur en argile (Fig. 3). La durée relativement longue de l'incubation en cabinet de croissance permet donc de mettre en évidence ce facteur secondaire dans l'expérience, mais néanmoins important. En cabinet de croissance, les pots étaient soumis à l'action régulière de l'eau, contrairement aux substrats incubés dans des erlenmeyers scellés au laboratoire dont la structure n'est pas altérée par l'eau. Cette différence importante contribue à expliquer la capacité de l'expérience en cabinet de croissance à mieux mettre en évidence l'effet de la texture du sol. Dans une étude de la survie et de la germination carpogénique des sclérotes en pots, mais au champ, Mitchell et Wheeler (1990) ne rapportaient pas de différence entre un sol argileux et un sol sableux et insistaient sur l'impossibilité d'extrapoler les résultats de telles études d'un sol à l'autre. Concernant l'association des apothécies avec la teneur en sable, l'ACR renforce le caractère réceptif (Alabouvette, 1986) du sable pour la germination carpogénique alors que l'analyse univariable montrait une interaction entre le type de substrat et la stérilisation qui ne permettait pas d'identifier clairement la relation entre la texture du substrat et la germination carpogénique.

En conclusions, les résultats des deux expériences en conditions contrôlées ont montré un effet suppressif du compost urbain seul ou en mélange avec les sols. Cet effet suppressif s'exprimait par une nette réduction de la survie dans les deux expériences et par une réduction de la production d'apothécies en cabinet de croissance. Ces résultats corroborent l'effet suppressif contre le *S. sclerotiorum* des composts (Nakasone et *al*., 1999) ou d'autres amendements organiques (Kokalis-Burelle et Rodriguez-Kabana, 1994; Viana et *al*., 2000) précédemment rapporté en conditions contrôlées ou au champ (Asirifi et *al*., 1994). De plus, l'effet de la stérilisation des substrats en cabinet de croissance confirme la nature biologique des phénomènes de suppression, hypothèse avancée par la plupart des auteurs qui étudient ces effets chez le *S. sclerotiorum* (Asirifi et *al*., 1994; Kokalis-Burelle et Rodriguez-Kabana, 1994; Nakasone et *al.*,1999; Tokeshi et *al*., 1997; Viana et

al., 2000) et autres *Sclerotinia* spp. (Lumsden et *al*., 1986; Wong et Willetts, 1975). Pour la première fois, l'association d'une méthode de respirométrie (Annexe A) et de comptages bactériens (Rusch, 1972) est couplée à une expérience évaluant la survie des sclérotes. Ces mesures ont permis de relier directement l'abondance bactérienne (estimée par les comptages) et l'effet suppressif de la MO sur la survie des sclérotes et ainsi de préciser la nature générale de la suppression, selon la définition de Rovira et Wildermuth (1981). De plus, la mesure du quotient de minéralisation du carbone (QMC) semble montrer qu'en plus de l'effet direct de la fraction labile de la MO sur l'abondance bactérienne, la faible proportion de MO stable par rapport à la MO labile rencontrée dans les sols seuls (QMC plus élevé) est favorable à la survie et à la germination carpogénique du *S. sclerotiorum*.

Tableau 1: Variables physico-chimiques et microbiologiques et méthodes de caractérisation des sols et du compost urbain des expériences en conditions contrôlées sur la survie et la germination carpogénique des sclérotes du *Sclerotinia sclerotiorum*.

Variable	Unité de mesure	Abréviation	Méthode/Source
Physique			
Argile	%	-	Gee et Bauder, 1986
Limon	%	-	Gee et Bauder, 1986
Sable	%	-	Gee et Bauder, 1986
Matière organique	%	MO	CPVQ, 1988
Humidité équivalente (capacité au champ)	%	Heq	Cassel et Nielsen, 1986
Chimique			
pH	-	pH	
Capacité d'échange cationique	$meqL^{-1}$	CEC	AFEQ, 1990
Carbone total	%	C	LECO CNS 2000 ®
Azote total	%	N	LECO CNS 2000 ®
Rapport carbone : azote	-	C/N	-
Souffre total	%	S	LECO CNS 2000 ®
Phosphore	ppm	P	Mehlich III
Potassium	ppm	K	Mehlich III
Calcium	ppm	Ca	Mehlich III
Magnésium	ppm	Mg	Mehlich III
Aluminium	ppm	Al	Mehlich III
Microbiologique			
Quotient de minéralisation du carbone	-	QMC	Respirométrie adaptée par Rousseau et Schaefer, 2003
Comptages directs solution physiologique	10^6 cellules·mL^{-1}	Comptages 1	Rusch, 1972
Comptages directs solution physiologique+5 $g·L^{-1}$ lactose/dextrose	10^6 cellules·mL^{-1}	Comptages 2	Rusch, 1972

Tableau 2: Variables physico-chimiques et microbiologiques des substrats d'incubation des sclérotes du *Sclerotinia sclerotiorum* au laboratoire et en cabinet de croissance.

Substrat	Caractéristiques des substrats d'incubation																
	Granulométrie			Physique		Chimie										Microbiologie	
	Argile	Limon	Sable	MO	Heq	pH	CEC	C	N	C/N	P	K	Ca	Mg	Al	QMC	Comptages 2
	%	%	%	%	%		meqL-1	%	%		ppm	ppm	ppm	ppm	ppm	41 j	10^6cellules·mL^{-1}
Compost urbain	0,0e	0,0e	0,0e	39,9a	87,1a	7,4a	37,5a	24,6a	1,66a	14,9a	158b	996a	5687a	487a	43e	0,014d	2825a
Loam argileux	27,5b	30,2b	42,4c	2,5d	33,8c	6,2d	17,8c	1,0e	0,08e	12,5c	50d	187c	1744d	307b	808b	0,16a	115d
Loam argileux+compost	30,9a	30,8a	38,3d	8,5b	40,2b	7,2b	23,4b	4,8b	0,39b	12,3c	162b	650b	3561b	-	502d	0,07c	405c
Loam sableux	8,3d	17,3c	74,4a	2,7d	23,4e	6,9c	13,1d	1,6d	0,10d	14,7a	225a	167c	1937c	107d	1054a	0,10b	102e
Loam sableux+compost	13,1c	15,1d	71,8b	7,2c	28,6d	7,3a	23,1b	4,5c	0,33c	13,7b	-	700b	3613b	206c	753c	0,07c	593b

Dans les colonnes, les substrats suivis de la même lettre ne sont pas significativement différents (contrastes qualitatifs, $P < 0,05$).

QMC à 41 j : quotient de minéralisation du carbone = (C du CO_2 / C total du sol) x100 (Dommergues, 1960)

Comptages 2: comptages directs de cellules bactériennes après 48 h d'incubation à 28˚C dans une solution physiologique à 5 g·L^{-1} Lactose/Dextrose (adaptée de Rusch, 1972).

(-) données manquantes.

Tableau 3: La survie des sclérotes (%) du *Sclerotinia sclerotiorum* après 41 j d'incubation au laboratoire, en fonction de deux sols, de l'amendement en compost urbain et de la stérilisation.

Stérilisation du substrat	**Substrat**					
	Compost urbain	**Loam argileux**	**Loam argileux + compost urbain**	**Loam sableux**	**Loam sableux + compost urbain**	**Moyenne des stérilisation**
			Survie des sclérotes (%)			
Stérilisé	25,0	35,0	35,0	38,3	30,0	32,7
Non stérilisé	23,3	41,7	21,7	35,0	25,0	29,3
Moyenne des substrats	24,2b	38,3a	28,3b	36,7a	27,5ab	

Les valeurs des substrats suivies de la même lettre ne sont pas significativement différentes (contrastes qualitatifs, $P < 0,05$).

Tableau 4: La survie (%) ou la germination carpogénique des sclérotes du *Sclerotinia sclerotiorum* après 4 et 18 mois en chambre de croissance, en fonction de deux sols, de l'amendement en compost urbain et de la stérilisation des substrats.

Stérilisation	**Substrat**					
du substrat	**Compost urbain**	**Loam argileux**	**Loam argileux + compost urbain**	**Loam sableux**	**Loam sableux + compost urbain**	**Moyenne des stérilisations**
			Survie à 4 mois (%)			
Stérile	13,3	66,7	30,0	66,7	45,0	44,3a
Non-stérile	10,0	40,0	15,0	56,7	20,0	28,3b
Moyenne	11,7bc	53,3a	22,5b	61,7a	32,5b	
			Survie à 18 mois (%)			
Stérile	1,7	21,7	5,0	5,0	0,0	6,7
Non-stérile	3,3	13,3	1,7	1,7	0,0	4,0
Moyenne	2,5b	17,5a	3,3b	3,3b	0,0c	
			Germination carpogénique (nombre total d'apothécies après 18 mois)			
Stérile	1,0b	3,7a	0,7b	1,0b	2,7a	1,8
Non-stérile	0,0c	4,3a	1,0b	9,7a	0,7b	3,1
Moyenne	0,5	4,0	0,8	5,3	1,7	

Les valeurs suivies de la même lettre ne sont pas significativement différentes (contrastes qualitatifs, $P < 0,05$).
Dans la colonne Moyenne des Stérilisations, les valeurs moyennes suivies de la même lettre ne sont pas significativement différentes (contrastes qualitatifs, $P < 0,05$).

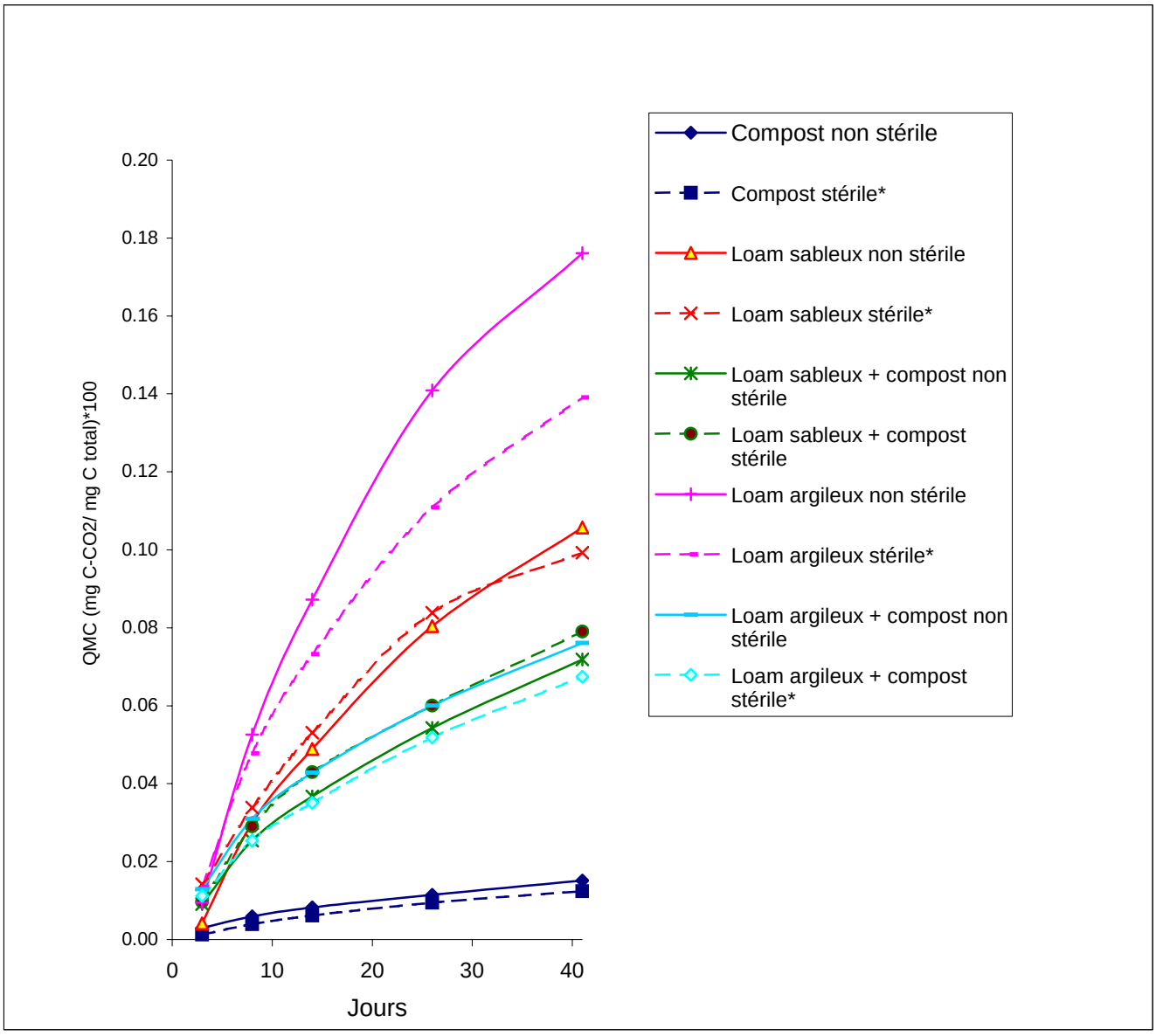


Figure 1: Dynamique du quotient de minéralisation du C (QMC) au cours de l'incubation de compost urbain, de loam argileux et de loam sableux, seuls ou en mélange, stériles ou non-stériles au laboratoire pendant 41 j à l'obscurité. Dans le cadre des légendes, l'astérisque (*) indique que le QMC du substrat stérile diffère significativement ($P < 0,05$) du QMC du substrat non-stérile correspondant, au 41^{e} j de l'expérience.

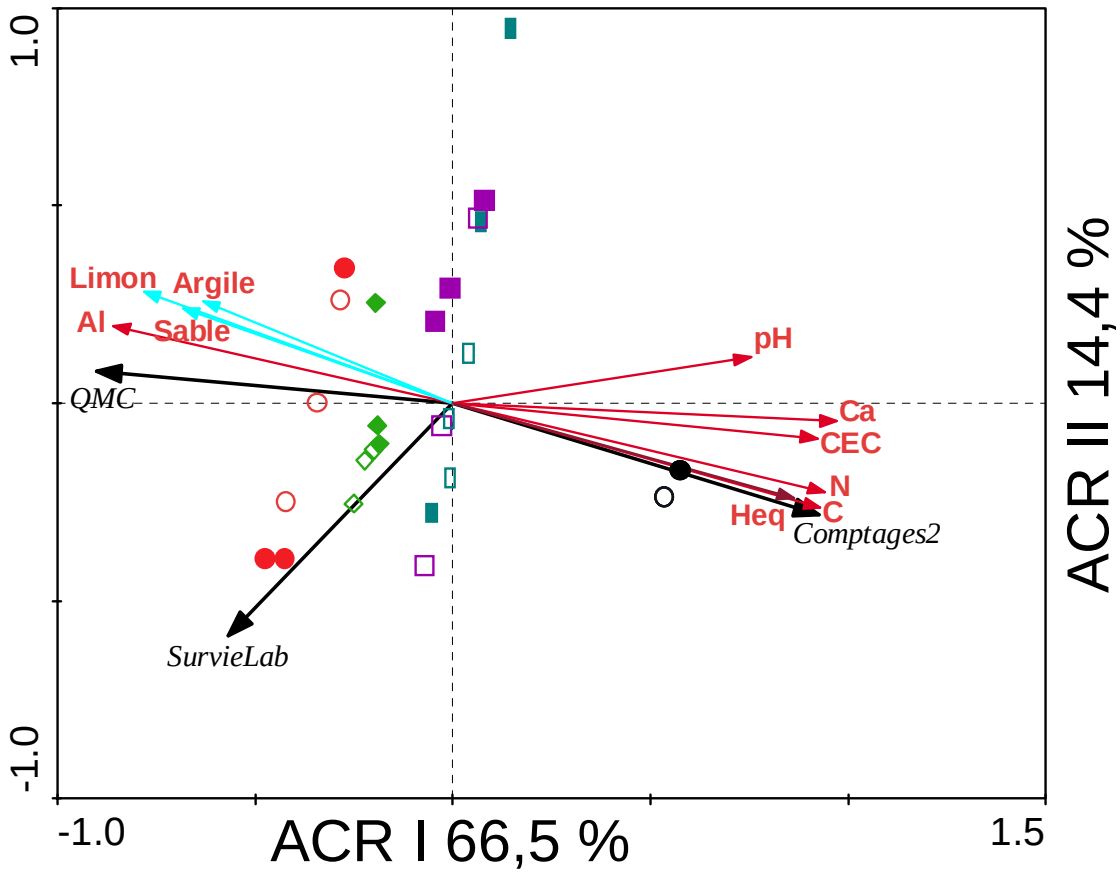


Figure 2 : Analyse canonique des redondances (ACR) qui explique la survie des sclérotes du *Sclerotinia sclerotiorum* (*SurvieLab*) après 41 j d'incubation au laboratoire dans cinq substrats stérilisés ou non, le quotient de minéralisation du carbone (*QMC*) et le nombre de cellules bactériennes par mL de suspension (*Comptages 2*) (Matrice Y des variables explicatives; flèches noires). Ces variables sont expliquées par des variables de physico-chimie du sol: granulométrie (argile, limon, sable; flèches bleues), humidité équivalente (Heq), pH, carbone (C), azote (N), calcium (Ca) et capacité d'échange cationique (CEC) (Matrice X des variables environnementales; flèches rouges). Les deux premiers axes canoniques (ACR I et II) expliquent respectivement 66,5 % et 14,4 % de la variance de la matrice Y. Ce modèle est significatif selon le test par permutations de Monte Carlo (999 permutations) (P = 0,001). Les objets sont classés d'après le substrat et la stérilisation: ○ compost urbain stérile; ● compost non-stérile; ◊ loam sableux stérile; ♦ loam sableux non-stérile; ○ loam argileux stérile; ● loam argileux non-stérile; ▯ loam sableux + compost urbain stérile; ▮ loam sableux + compost non-stérile; □ loam argileux + compost stérile; ■ loam argileux + compost non-stérile.

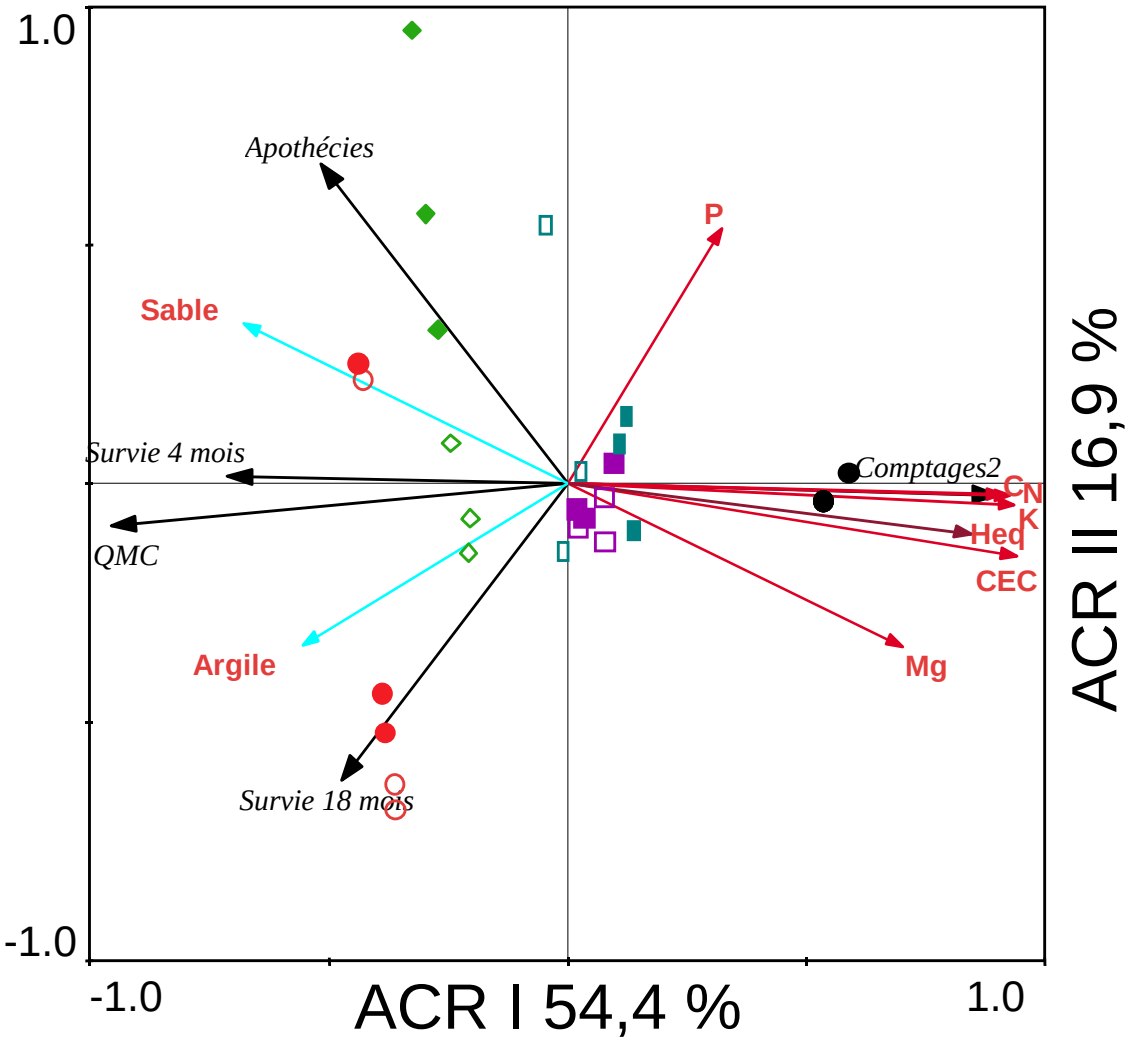
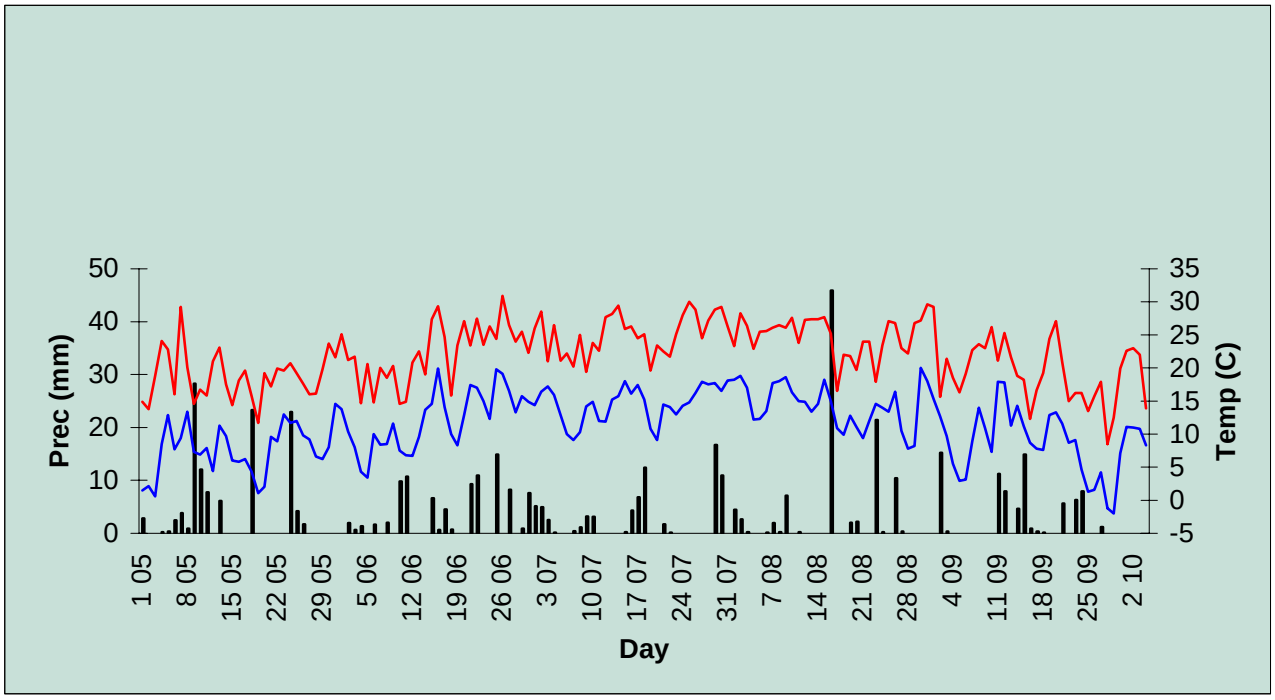
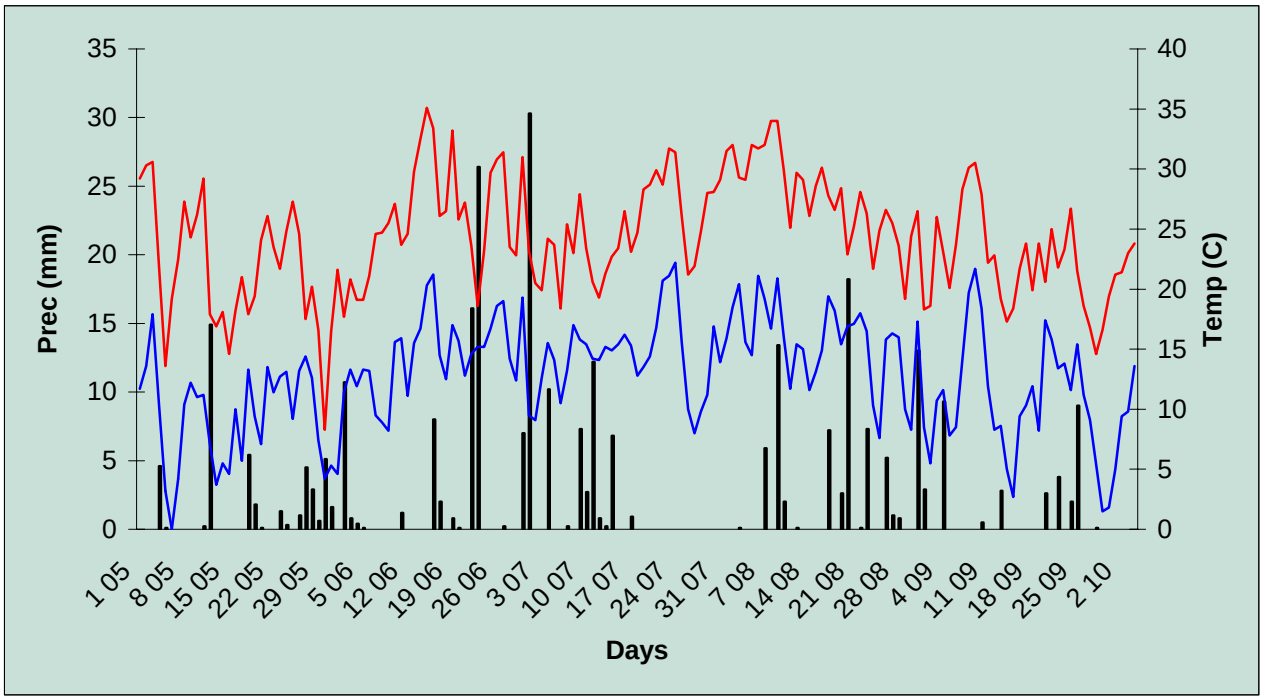


Figure 3 : Analyse canonique des redondances (ACR) qui explique la survie des sclérotes du *Sclerotinia sclerotiorum* après 4 et 18 mois d'incubation en cabinet de croissance (*Survie 4 mois et 18 mois*) et leur production d'apothécies (*Apothécies*) dans cinq substrats stérilisés ou non, ainsi que le quotient de minéralisation du carbone (*QMC*) et le nombre de cellules bactériennes par mL de suspension (*Comptages 2*) (Matrice Y des variables explicatives; flèches noires). Ces variables sont expliquées par des variables de physico-chimie du sol: granulométrie (argile, sable; flèches bleues), humidité équivalente (Heq), carbone (C), azote (N), phosphore (P) potassium (K), magnésium (Mg) et capacité d'échange cationique (CEC) (Matrice X des variables environnementales; flèches rouges). Les deux premiers axes canoniques (ACR I et II) expliquent respectivement 54,4 % et 16,9 % de la variance de la matrice Y. Ce modèle est significatif selon le test par permutations de Monte Carlo (999 permutations) (P = 0,001). Les objets sont classés d'après le substrat et la stérilisation: ○ compost stérile; ● compost non-stérile; ◊ loam sableux stérile; ♦ loam sableux non-stérile; ○ loam argileux stérile; ● loam argileux non-stérile; □ loam sableux + compost stérile; ▮ loam sableux + compost non-stérile; □ loam argileux + compost stérile; ■ loam argileux + compost non-stérile.

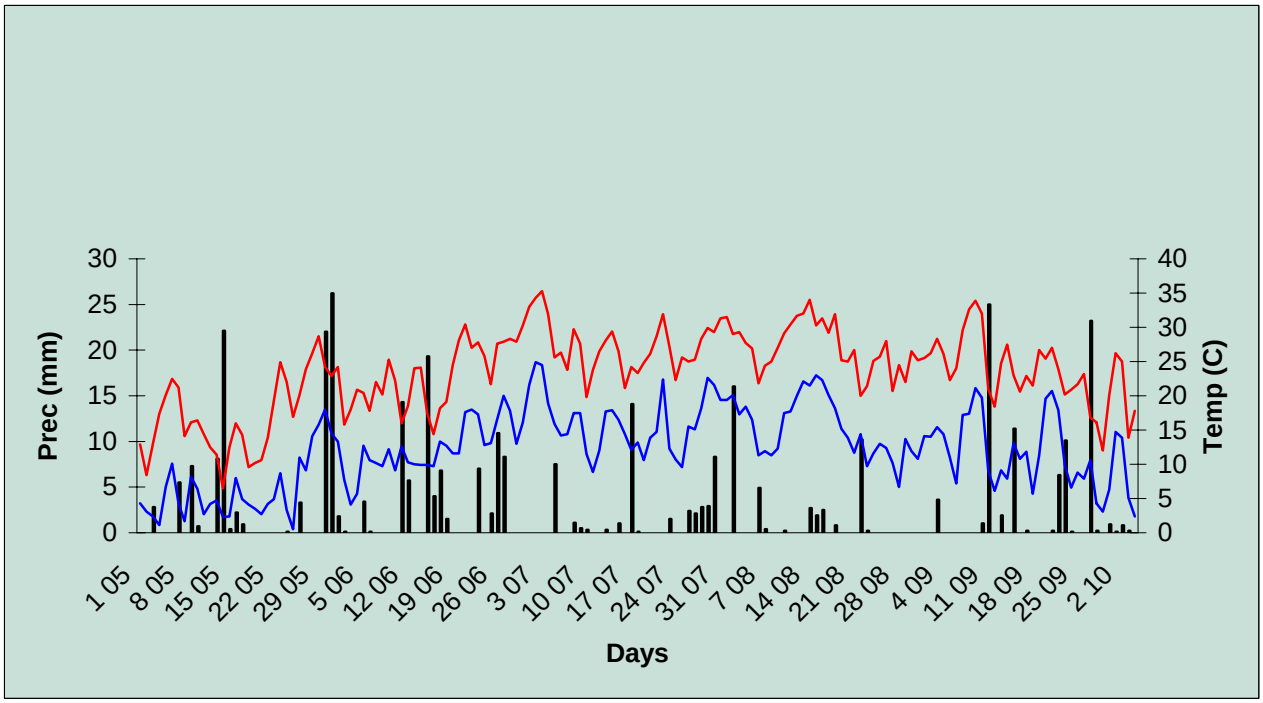
ANNEXE D: Précipitations et températures journalières à la station IRDA-CÉROM de Saint-Hyacinthe en 2000 (a), 2001 (b) et 2002 (c)



a. The daily rainfall (Prec) and temperature (Temp with red line for maxima and blue line for minima) for the Saint-Hyacinthe (Québec) IRDA-CÉROM research station in 2000.



b. The daily rainfall (Prec) and temperature (Temp with red line for maxima and blue line for minima) for the Saint-Hyacinthe (Québec) IRDA-CÉROM research station in 2001.



c. The daily rainfall (Prec) and temperature (Temp with red line for maxima and blue line for minima) for the Saint-Hyacinthe (Québec) IRDA-CÉROM research station in 2002.